Estructura y funcionamiento de ecosistemas secos del Sur de Ecuador

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Estructura y funcionamiento de ecosistemas secos del Sur de Ecuador.

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CERTIFICAN:

Que los trabajos de investigación desarrollados en la memoria de tesis doctoral: "**Estructura y funcionamiento de ecosistemas secos del sur del Ecuador**", son aptos para ser presentados por el Ldo. Carlos Iván Espinosa Iñiguez ante el Tribunal que en su día se consigne, para aspirar al Grado de Doctor por la Universidad Politécnica de Madrid.

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Dr. Marcelino de la Cruz Rot

Dr. Adrian Escudero Alcántara

A mi familia; mis hijos, mi esposa que

son la verdadera razón de mi vida.

Yo vivo de preguntar,
saber no puede ser lujo…

Si saber no es un derecho,
seguro será un izquierdo……

Silvio Rodríguez

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Índice

Resumen

En la actualidad, los bosques secos neotropicales se encuentran restringidos a una pequeña fracción de su área de distribución histórica, debido principalmente a la acelerada pérdida de cobertura vegetal. Es por esta razón que son reconocidos como uno de los ecosistemas más amenazados del mundo. Durante las últimas décadas estos bosques han recibido mayor atención por parte de investigadores, y pese a que el esfuerzo dedicado al estudio y conocimiento de estos bosques no es comparable al de otros bosques de la región, especialmente los ligados a las pluviselvas húmedas, los trabajos llevados a cabo fundamentalmente por botánicos han permitido describir una buena parte de su diversidad florística en amplias regiones del neotrópico, constatar el elevado nivel de endemicidad de su flora y determinar algunos de los factores que determinan su estructura y funcionamiento. Sin embargo, aún existen regiones como la denominada *Pacífico Ecuatorial* donde la investigación ha sido escaza. El conocimiento de la diversidad biológica así como cuáles son los factores que controlan el funcionamiento y la estructuración de estos bosques resultan prioritarios para poder desarrollar acciones de conservación efectivas. El presente trabajo aporta a la comprensión del funcionamiento de dos sistemas secos tropicales de la región del *Pacífico Ecuatorial* el matorral seco y el bosque seco del sur del Ecuador.

Se estableció una parcela de 9ha en bosque seco con el fin de evaluar asociaciones intraespecíficas e interespecíficas, se registró la diversidad y abundancia de todas las especies leñosas con un dap igual o superior a 5cm, además se obtuvo la ubicación espacial de cada individuo. Adicionalmente se realizaron 109 parcelas a lo largo de 4 de los cantones de la provincia de Loja que conservan en buen estado bosques secos. En el matorral seco se desarrollo un estudio observacional a lo largo de una gradiente estrés climático y dos niveles de manejo no disturbado y pastoreado. En cada nivel se colocaron 2 parcelas dentro de las cuales se registró la abundancia, diversidad y cobertura de todas las especies anuales. Además, se tomaron 9 muestras de suelo en cada parcela para evaluar el banco de semillas del suelo.

Los resultados muestran que el bosque seco las relaciones positivas planta-planta juegan un papel fundamental en la estructura florística de las comunidades. Así se pudo observar que a escalas regionales la disponibilidad de agua tiene una relación inversa con la riqueza, encontrándose que áreas con menor disponibilidad de agua generan comunidades vegetales más diversas. Esta respuesta es coherente con la Hipótesis de la Gradiente de Estrés ya que el incremento de las relaciones de facilitación estaría incrementando la cantidad de especies que coexisten a nivel local. Por otro lado a escalas locales las especies de bosque seco tropical muestran un bajo grado de agrupamiento con sus congéneres, lo cual coincide con la propuesta de la "*Dependencia Negativa de la Densidad*" propuesta por Janzen – Connell. Esta respuesta contribuye al

comportamiento acumulador de especies observado en el bosque seco, por lo observado en este trabajo a escalas locales las interacciones positivas planta-planta son predominantes.

En el matorral seco montano los resultados muestran que la magnitud de los efectos de las especies ingenieras del ecosistema en la diversidad de especies y la productividad varían a lo largo de gradientes ambientales y a con la escala espacial de la comunidad. Así, en las zonas con mayor presión ambiental y una mayor presión de pastoreo, el efecto de las plantas ingenieras es mayor. Por otro lado, se pudo observar que la estabilidad de la diversidad en la escala de la comunidad parece ser la norma con efectos nulos de los factores de estrés en las propiedades de la comunidad. A nivel de microhábitat la importancia de la facilitación incrementa cuando los factores de estrés climático aumentan, y bajo las copas de Croton la diversidad y la cobertura es mayor que en el suelo desnudo, esta diferencia se incrementa con el estrés abiótico. Esta respuesta fue modulada por el pastoreo, en las zonas más altas con menor estrés climático, la facilitación se mantuvo debido a que la competencia se reduce por efecto del pastoreo, ya que las manchas se transforman refugios libres de herbivoría. Así, el estrés biótico por los consumidores altera significativamente la naturaleza y la fuerza de las interacciones entre especies en las comunidades, e incluso puede cambiar el signo de las interacciones entre especies.

El banco de semillas muestra una importante interacción entre los factores de estrés, los efectos en el banco de semillas del suelo se explica mejor cuando los factores de estrés, tanto climáticos y el pastoreo son evaluados. En condiciones inalteradas la riqueza y abundancia del banco de semillas aumenta con la altitud y se reduce el estrés. Este patrón es modulado por el pastoreo, en el extremo inferior del gradiente altitudinal, el pastoreo produce un aumento en la riqueza y la densidad del banco de semillas y en el extremo superior del gradiente altitudinal el pastoreo reduce estos dos atributos.

Abstract

Currently, Neotropical dry forests are restricted to a small fraction of their historic range, primarily due to the accelerating loss of plant cover. It is for this reason they are recognized as one of the world's most threatened ecosystems. In recent decades, these forests have received increased attention from researchers, despite the effort devoted to the study and knowledge of these forests is not comparable to other forests in the region, especially those linked to wet rainforests, the work carried out mainly by botanists, have allowed to describe a good part of floristic diversity in large regions of the Neotropics, verify the high level of endemic flora and identify some of the factors that determine their structure and function. However, there are regions little known as the Equatorial Pacific where research has been scarce. Knowledge of biodiversity and the factors that control the operation and structure of these forests are priorities to develop effective conservation action. This work contributes to understanding the functionality of two tropical dry systems the Pacific Equatorial; Dry scrub and dry forest of southern Ecuador.

We established a 9Ha plot in dry forest in order to assess intraspecific and interspecific associations, we recorded the diversity and abundance of all woody species with dbh higher than 5 cm, in addition we obtained the spatial location of each individual. We performed 109 plots along 4 districts in the province of Loja, these districts have a well preserved dry forests. In dry scrub, we developed an observational study along a climatic stress gradient and two levels of management; grazed and undisturbed. At each level were placed 2 plots within which we recorded the abundance, diversity and coverage of all annual species. In addition, 9 samples of soil taken from each plot to evaluate the soil seed bank.

The results show that in dry forest the positive plant-plant relationships play a key role in determine the floristic structure of communities. Thus at regional scales, we observed that water availability is inversely related to richness, we found that areas with lesser availability of water generate more diverse plant communities. This response is consistent with the stress gradient hypothesis, an increase in facilitation could be increased the number of species to coexist locally. In addition, at local scales, the tropical dry forest species show a low degree of clustering with conspecifics, which agrees with the proposal of "Negative Density Dependence" proposed by Janzen - Connell. This response contributes accumulator species behavior observed in the dry forest, so at local scales, the positive plant-plant interactions are predominant interaction.

In tropical dry scrub our results support our expectations since the magnitude of the effects of ecosystem engineers/nurse in species diversity and productivity vary along environmental gradients and at contrasting spatial community scales. Thus in zones

with higher environmental stress and higher grazing pressure, the engineering plants effect is higher. Diversity stability at the whole community scale seems to be the norm with null effects of stressors on some community properties in spite of the existence of net effects when they are surveyed at smaller community scales such as the pair-wise differences between nurse and open areas. As expected our study demonstrates that climate acted as a key environmental filter in soil seed bank development and structure and also that grazing modulated the effect of climate on seed bank properties. In this tropical dry scrub, richness and abundance of seeds increased along the altitudinal gradient, most likely because ascending in altitude environmental conditions are improved.

Introducción

Los "Bosques tropicales estacionalmente secos" (*sensu* Murphy y Lugo 1995) comprenden bosques deciduos y semi-deciduos que crecen en áreas tropicales sujetas a una severa estacionalidad climática, marcada por un periodo de sequía que se prolonga hasta 5 o 6 meses al año, determinando una de las características más conspicuas de esta formación; la pérdida estacional de las hojas y del bosque en general con una época sin hojas durante la estación seca y una fisionomía de bosque siempre verde a lo largo de la estación lluviosa. Esta definición es bastante amplia y permite la inclusión de diversas formaciones vegetales que van desde matorrales espinosos hasta bosque deciduos y semideciduos (Murphy & Lugo, 1995). Los avances obtenidos en el conocimiento de los bosques secos durante los últimos años han mostrado las relaciones biogeográficas de los diferentes núcleos y su funcionamiento. La presente tesis plantea realizar una revisión de los avances alcanzados durante los últimos años en estos bosques evaluando los vacios de información que existen, para ello planteamos el capitulo 1 ***"Bosques secos del neotrópico: diversidad, estructura, funcionamiento e implicaciones para la conservación"***.

Dentro de los diferentes núcleos de bosque seco neotropical la ecoregión Tumbes-Piura y bosque seco ecuatoriano ha sido definida como una única región fitogeográfica denominada *Ecuatorial del Pacífico* (Peralvo et al. 2007). Esta región es una de las zonas de endemismo más importante en el mundo (Davis et al. 1997). Esta característica determinó que esta área junto con los bosques del Chocó colombiano y ecuatoriano conformaran el denominado "Tumbes-Chocó-Magdalena Hotspot" (Mittermeier et al. 2005). Además, en esta zona confluye la denominada "Región Tumbesina" que es una de las Áreas de Endemismo de Aves (EBAs) más importantes y amenazadas de todas las EBAs a nivel global (Best and Kessler 1995, Leal-Pinedo and Linares-Palomino 2005).

En Ecuador las zonas de bosque seco están incluidas en las formaciones de la costa, en las subregiones Centro y Sur (Sierra 1999) desde la Provincia de Esmeraldas y los Ríos al Norte en Ecuador hasta Lambayeque y Libertad al Sur del Perú (Aguirre et al.

2006b). En la provincia de Loja se encuentra la mayor superficie de este ecosistema, que incluyen las tierras bajas, estribaciones occidentales bajas de la cordillera de los andes y los valles secos interandinos del sur (Aguirre and Kvist 2005). Los boque secos del Sur del Ecuador y Norte del Perú están caracterizados por poseer una alta diversidad y una extraordinaria cantidad de especies endémicas de diferentes grupos taxonómicos (Best and Kessler 1995, Linares-Palomino et al. 2010, 2011)

A pesar de la importancia de estos bosques son poco conocidos y la mayoría de investigación no ha sido publicada y lamentablemente se encuentra como literatura gris (Aguirre et al. 2006b), sin embargo se han realizado importantes avances en el conocimiento florístico de esta zona gracias a estudios desarrollados en Ecuador y Perú (Aguirre and Kvist 2005, Aguirre et al. 2006a, 2006b, Linares-Palomino et al. 2010)

Varias aproximaciones para establecer formaciones vegetales en base a su afinidad florística han sido desarrollados (Aguirre and Kvist 2005, Aguirre et al. 2006a, 2006b), pudiéndose destacar 3 formaciones claramente establecidas; *matorral seco espinoso*, *bosque seco deciduo* y *bosque seco semideciduo*.

El *matorral seco espinoso* ocurre en las tierras bajas en terrenos de relieve plano con presencia de algunas colinas (Aguirre et al. 2006b) y en las partes más secas y cálidas, en general cerca y a menudo continuas al Océano Pacífico (o los manglares), sin embargo, en Loja se encuentra esta formación en los valles interandinos a mayor altitud en áreas con fuertes pendientes. Casi todas las especies pierden sus hojas durante la estación seca (Aguirre et al. 2006a). La vegetación es poco densa, aislada, xerofítica, espinosa, achaparrada con presencia de cactus columnares y plantas con látex de los géneros Capparis, Croton y Euphorbia (Aguirre et al. 2006a, 2006b).

El *bosque seco deciduo* ocurre en las tierras bajas entre 0 y 700 m, se encuentra ubicado en Ecuador en las provincias de Manabí, Guayas, El Oro y Loja (Aguirre et al. 2006a). La característica predominante es que más del 75% de sus especies pierden las hojas durante la estación seca (Aguirre et al. 2006a, 2006b). Los elementos característicos de esta formación son *Ceiba trichistandra* entre otras Bombacaceae, *Tabebuia chrysantha* y *Tabebuia billbergii* (Aguirre et al. 2006b).

El *bosque seco semideciduo* ocurre en altitudes que van desde los 200 a los 1100 m en zonas de colinas, donde existe mayor humedad que los bosques deciduos (Aguirre et al. 2006a). Localizado sobre laderas con pendientes moderadas de entre 40-50 %, en suelos muy pedregosos (Aguirre et al. 2006b). Entre el 75 y 25% de los elementos florísticos que conforman este tipo de bosque pierden sus hojas en la temporada seca (Aguirre et al. 2006a, 2006b). El estrato superior alcanza aproximadamente los 20 m de altura y algunos elementos característicos son: *Centrolobium ochroxylum*, *Phytolacca dioca*, *Triplaris cumingiana*, *Cochlospermum vitifolium* y *Gallesia integrifolia* (Aguirre et al. 2006a, 2006b).

En cuanto a la diversidad de la flora de especies leñosas (en alguna de sus etapas de desarrollo alcanza los 3m) Aguirre et al. (2006) en un estudio que recoge información florística levantada en los dos países reporta un total 65 familias con 313 especies leñosas para los bosques estacionalmente secos de Ecuador y Perú. De estas 85 especies están presentes en el denominado matorral seco espinoso, 215 en el bosque seco deciduo, y 198 en el bosque seco semideciduo. A nivel de país las especies forestales se reparten con 103 especies reportadas en ambos países, 239 especies para Ecuador y 177 para Perú. Como en el caso de la diversidad se observa una mayor cantidad de especies reportadas solo para Ecuador 136, mientras que Perú reporta 74 especies únicas para ese país (Aguirre et al. 2006b)

La región *Ecuatorial del Pacífico* puede ser dividida en tres partes de acuerdo a su afinidad florística, el grupo más afín lo conforman Manabí, Guayas, El Oro, Loja y Tumbes. Un segundo grupo lo conforman Esmeraldas y Los Ríos y el tercer grupo lo conforman Piura, Cajamarca, Lambayeque y La Libertad (Aguirre et al. 2006b). Posiblemente las diferencias florísticas estén correlacionadas con el grado de disponibilidad de agua. El segundo grupo se encuentra cercano a la zona del Chocó lo cual estaría incrementan la disponibilidad de agua, el tercer grupo se encuentra en la zona de influencia de la corriente fría de Humbolt, que genera una disminución en las precipitaciones, finalmente el primer grupo se encontraría en una zona intermedia de humedad. Sin embargo, es necesario evaluar la influencia de estos factores en la agrupación de estas regiones.

La región *Pacifico Ecuatorial* es una de las zonas con mayor grado de endemicidad de las áreas de bosque seco después de las islas del Caribe (Best and Kessler 1995, Linares-Palomino et al. 2011). El alto grado de endemicidad dentro de esta área es explicada por el aislamiento que esta región presenta frente a los bosques secos de Centro América por la zona biogeográfica de selvas húmedas del Chocó, que constituye una barrera para las especies de climas más secos situados al norte (Best y Kessler 1995, Gentry 1995), además la presencia de los Andes causa el aislamiento de la región costera trans-andina del Pacífico (Davis et al., 1997; Rodriguez et al., 2004). Madsen et al. (2001), manifestaron que el endemismo florístico de los bosques estacionalmente secos del Ecuador es importante, ya que es parte del centro de endemismo de plantas áridas del Guayas, que se extiende desde la provincia de Manabí hasta el norte de Perú.

La menor diversidad comparada con los bosques lluviosos es claramente debido a los bajos niveles de diversidad dentro de las familias y géneros. Una excepción a esta norma es la familia Legminosae, la cual muestra altos niveles de diversidad en géneros (34 géneros, 19% del total), específico (70 especies, el 22% del total) y los niveles de endemicidad (15 especies endémicas, el 21% del total) (Linares-Palomino et al. 2010). Estos resultados han sido similares a los obtenidos en varios estudios que han demostrado que esta familia es una de las más prominentes de estos bosques (Gentry, 1995; Pennington et al 2006). Los patrones de endemicidad muestran ser opuestos a los patrones de diversidad, las especies endémicas muestran una importante disminución las regiones montañosas (Linares-Palomino et al. 2010).

Los avances realizados durante estos últimos años han permitido entender algunos de los procesos que participan en la estructuración de las comunidades vegetales en los ecosistemas estacionalmente secos del Neotrópico. La disponibilidad de agua sin lugar a dudas es uno de los factores limitantes más importantes en estos ecosistemas, siendo crítica para el establecimiento, supervivencia y desarrollo de las plantas (Ruthemberg 1980), condicionando tanto los gradientes espaciales (Balvanera et al. 2011), los procesos ecológicos básicos y las interacciones bióticas que se establecen en cada bosque (Martinez-Yrizar et al. 1992, Mooney et al. 1993). Además de la disponibilidad absoluta, la estacionalidad y la variación interanual de la precipitación marcan la

dinámica de las comunidades vegetales y la estructura florística en los BTES (Blain y Kellman 1991, Murphy y Lugo 1995, Sampaio 1995). En la región *Pacífico Ecuatorial* se han desarrollado importante avances en el conocimiento florístico de esta zona sin embargo entender cuáles son los factores que determinan la estructura florística ha sido poco explorado, nuestro segundo capítulo ***"What Factors Affect Diversity and Species Composition of Endangered Tumbesian Dry Forests in Southern Ecuador?"*** explora los factores ambientales que están influyendo en la composición florística y analiza los efectos de los factores climáticos en algunas de las propiedades de la comunidad vegetal.

Los patrones espaciales y los mecanismos potenciales asociados a los patrones no-aleatorios de distribución de especies a escala pequeña han sido poco estudiados en los bosques secos (Balvanera et al. 2011). A dichas escalas se ha observado en varios casos que la disponibilidad de agua restringe los patrones de distribución de muchas especies y en consecuencia filtran las especies que forman la comunidad (Balvanera et al. 2011). A pesar de la existencia de esta correlación entre la distribución de especies y disponibilidad de agua, a escalas regionales muchos autores no han encontrado relaciones significativas entre la diversidad y la disponibilidad de agua (Gentry 1995, Trejo y Dirzo 2002). En este sentido la existencia de interacciones positivas planta-planta permiten el mantenimiento de la diversidad, sobre todo bajo condiciones ambientales extremas como las observadas en el bosque seco, debido a que muchas especies pueden mejorar el medio ambiente para otras especies (Hacker and Gaines 1997, Callaway 1997, Wiegand et al. 2007a, Maestre et al. 2009). En el capítulo 3 ***"Species association and diversity structure in a Tropical Dry Forest"*** y capítulo cuatro ***"Diversity Stability at the whole Community Scale Depends on Plant to Plant Interactions Shifts along Co-occurring Stress Gradients in a Mountain Ecuadorian Dry Scrub Ecosystem"*** evaluamos el rol de las interacciones planta-planta en la estructura florística de dos de los ecosistemas secos del sur del Ecuador, el bosque seco y el matorral seco respectivamente.

En los bosques secos se encuentra aceptada que la importancia relativa de semillas y rebrotes en el reclutamiento depende de las condiciones climáticas. La regeneración por rebrote ("ramets" de genotipo idéntico al individuo "parental" (Ceccon et al. 2006)) en

muchas especies de árboles y arbustos es más importante que la regeneración por semillas (Murphy y Lugo 1986, Kauffman 1991, Rico-Gray y García-Franco 1992, Swaine 1992, Miller y Kauffman 1998). En sistemas tan estresantes climáticamente como el de los BTES este tipo de regeneración es favorecido, dado que el desarrollo a partir de brotes vegetativos puede aprovechar el extenso sistema de raíces y el almacenamiento de nutrientes en las partes restantes de la planta madre especialmente inmediatamente después de cualquier tipo de perturbación (Koop 1987, Negrelle 1995).

Finalmente en el capítulo 5 ***"Patch effect on soil seed bank is modulated by co-occurring stressors"*** evaluamos la importancia de los factores climáticos sobre la abundancia y diversidad del banco de semillas del matorral seco.

Objetivos

Objetivo General

La presente tesis tiene como objetivo general el evaluar el efecto de factores climáticos y las interacciones planta – planta sobre la diversidad de especies y la estructura de las comunidades vegetales del matorral seco y bosque seco del Sur del Ecuador. Además se evalúan como las actividades antrópicas modifican las respuestas de la comunidad.

Objetivos Específicos

- Establecer los avances logrados en los bosques secos neotropicales y definir los vacios de investigación (Capítulo 1)

- Determinar la influencia de factores regionales como el clima y locales como las características del suelo, la topografía y la degradación antropogénica afectan la composición y la diversidad de los bosques secos Tumbesinos (Capítulo 2).

- Evaluar el rol especies – específico sobre la estructuración espacial de la diversidad y la importancia de las interacciones espaciales planta – planta en una comunidad de bosque seco (Capítulo 3).

- Estudiar la importancia relativa de distintos mecanismos de interacción planta - planta a la hora de determinar la riqueza local de especies en la comunidad de matorral seco y su respuesta a la co-ocurrencia de estresores climáticos y de herbivoría (Capítulo 4).

- Entender el efecto de los parches de vegetación en las propiedades del banco de semillas del suelo y como estos reservorios son afectados por filtros bióticos (herbivoría) y abióticos (climáticos) (Capítulo 5).

Metodología general y área de estudio

Área de estudio

La presente tesis fue desarrollada en dos ecosistemas semiáridos distintos; el denominado bosque estacional seco tropical (capítulos 2 y 3) y el matorral seco montano (capítulos 4 y 5). Estos ecosistemas en el Ecuador son parte de la región Tumbesina (Dinerstein et al. 1995), que es reconocida como uno de los puntos más amenazados del mundo y probablemente uno de los menos conocidos (Janzen 1988). La Región Tumbesina abarca una estrecha franja de tierra entre el Océano Pacífico y los Andes, abarcando los territorios del suroeste de Ecuador y el extremo noroeste del Perú. La Región Tumbesina abarca altitudes desde el nivel del mar hasta los 2000m alcanzando en algunos puntos altitudes máximas de 3000m, esta región abarca 87.000 km2 (Best & Kessler 1995, Dinerstein et al., 1995).

El bosque estacional seco, se caracteriza por la llamada ceiba (*Ceiba trichistandra*) y sus familiares (Bombacaceae Aguirre et al. 2006). Estos bosques son muy ricos en especies y refugio de una extraordinaria diversidad de endemismos de muy diferentes grupos taxonómicos (Best & Kessler 1995). El trabajo en el bosque seco se llevo a cabo en dos áreas de estudio el capítulo 2 estableció como área de estudio casi 1864km2 en la provincia de Loja (cantones Zapotillo, Macará, Celica; 120-2640masl) en uno de los remanentes más grandes y mejor conservados de los bosques secos Tumbesinos (Aguirre y Kvist 2005). En todo este vasto territorio, la gestión de la tierra ha sido de baja intensidad durante la última década por lo que esta zona se encuentra relativamente bien conservada. La temperatura media anual en la región es de unos 24°C (rango: 10-33°C) y con una precipitación media anual de 500 mm / año. Estos bosques secos son el hábitat de varias especies en peligro de extinción como *Juglans neotropica* (Juglandaceae), *Siparuna eggersii* (Monimiaceae). El capítulo 3 fuel llevado a cabo en la Reserva Ecológica Arenillas (REMA), está reserva se encuentra situada en el extremo sur del Ecuador, provincia de El Oro, entre las ciudades de Arenillas y Huaquillas, y cubre un área de 16.958 ha, con un rango de altitud 0 a 300 m. El clima se caracteriza por una estación de lluvias de cuatro meses con una precipitación media anual de 515

mm a partir de enero a abril y de 152 mm durante la estación seca. La temperatura media 25.2°C tienen una variación máxima de 3.4 º C entre los meses más fríos y más cálidos, la temperatura es más baja durante la estación seca.

Los capítulos 4 y 5 fueron desarrollados en el matorral seco montano, este ecosistema es una variante de los bosques secos Tumbesinos, en los valles inter-andinos a lo largo de un gradiente altitudinal de 1000 m (Espinosa et al. 2011). La temperatura media anual es de 27.5°C (Catamayo aeropuerto; 1500 m), la temperatura máxima media es de 30.8°C (en Octubre) y la temperatura media mínima es de 17.9 ° C (en Junio). La precipitación media y la evapotranspiración son 383 mm/año y 1112 mm/año, respectivamente (Richter & Moreira-Muñoz 2005). Entre mayo y diciembre las lluvias no compensa la evapotranspiración local, lo que provoca un déficit de agua intensa. El sustrato geológico está conformado por rocas metamórficas paleozoicas mezclados con rocas volcánicas y sedimentarias de los períodos Cretácico y Terciario. La vegetación constituye manchas de especies perennes intercaladas con áreas de tierra desnuda donde las plantas anuales son dominantes en invierno. Croton wagnerii (Müll) Arg. (Euphorbiaceae) es la especie dominante en la formación de matorral.

Metodología general

En esta tesis doctoral se han realizado experimentos observacionales, en los que en algunos casos se incluyen distintos niveles de estrés abiótico (clima) y biótico (herbivoría). Los diferentes niveles estrés climático se han conseguido mediante el uso de gradientes ambientales amplios. En estas se han homogeneizado, tanto como ha sido posible, la pendiente, orientación, tipo de suelo e historia de manejo previo de las parcelas seleccionadas, con la intención de evitar la influencia de otros factores que no estuvieran considerados en el experimento y que pudieran confundir la interpretación de resultados.

En el caso del bosque seco se establecieron 109 parcelas de 10x50m en la provincia de Loja en algunos de los sitios mejor conservados de la provincia y donde las presiones antrópicas son reducidas, estas parcelas nos permitieron desarrollar el capítulo 2. Para poder responder las preguntas planteadas en el capítulo 3 se estableció una parcela

permanente de 9ha en la reserva Arenillas (REMA). Todas las especies vegetales superiores a 5cm de DAP fueron registradas e identificadas, en el caso de la REMA, además se definió la ubicación espacial de todos los individuos.

En el matorral seco montano se establecieron dos localidades diferenciadas por el grado de herbivoría, Chinchas con herbivoría y Alamala sin herbivoría. En cada localidad, el rango altitudinal ocupado por Croton fue dividido para ubicar cuatro sitios. Se establecieron dos parcelas de 30 x 30 m en cada sitio, separados por no más de 500 m de distancia horizontal (distancia media fue de 200 m). Cada parcela se encuentra ubicada en una porción representativa y homogénea de la zona de matorral, evitando barrancos, acantilados, y cualquier objeto/estructura que podría sesgar nuestras estimaciones de la diversidad taxonómica. En cada parcela se obtuvieron medidas de cobertura, abundancia diversidad de las especies perennes, además se muestreo el banco de semillas del suelo.

CAPÍTULO 1: BOSQUES SECOS DEL NEOTRÓPICO: DIVERSIDAD, ESTRUCTURA, FUNCIONAMIENTO E IMPLICACIONES PARA LA CONSERVACIÓN

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Resumen

Los bosques secos neotropicales son reconocidos como uno de los ecosistemas más amenazados del mundo. La acelerada pérdida de cobertura vegetal de estos bosques ha ocasionado que en la actualidad se encuentren restringidos a una pequeña fracción de su área de distribución histórica. Conocer su diversidad biológica así como cuáles son los factores que controlan el funcionamiento y la estructuración de estos bosques resulta prioritario para poder desarrollar acciones de conservación efectivas. Pese a que el esfuerzo dedicado al estudio y conocimiento de estos bosques no es comparable al de otros bosques de la región, especialmente los ligados a las pluviselvas húmedas, los trabajos llevados a cabo fundamentalmente por botánicos han permitido describir una buena parte de su diversidad florística en amplias regiones del neotrópico, constatar el elevado nivel de endemicidad de su flora, obtener algo de información sobre los factores que determinan su estructura y funcionamiento, así como esbozar cuales pueden ser las causas que los están empujando a la desaparición. En este trabajo se recogen los avances logrados en el conocimiento de este ecosistema al tiempo que se identifica los vacíos de información que deberían ser considerados como prioridad de investigación en el futuro próximo de cara a minimizar la tasa de destrucción o si cabe, al desarrollo de técnicas de restauración apropiadas. Así mismo se evalúan las principales amenazas

que sufren estos bosques y las implicaciones sobre la persistencia de los bosques secos del Neotrópico.

Palabras clave: diversidad, endemismo, funcionamiento, regeneración, conservación.

Introducción

El término "Bosques tropicales estacionalmente secos" (BTES) fue acuñado por Murphy y Lugo (1995) y es utilizado también para los bosques secos del Neotrópico (Mayle 2004) que es el sentido que daremos al acrónimo a lo largo de este trabajo. Los BTES comprenden bosques deciduos y semi-deciduos que crecen en áreas tropicales sujetas a una severa estacionalidad climática, marcada por un periodo de sequía que se prolonga hasta 5 o 6 meses al año durante los que la precipitación es inferior a 100mm/m2. La precipitación media a lo largo de todo el año es inferior a 1600 mm/m2 (Gentry 1995) y la proporción precipitación/evapotranspiración menor que 1 (Dirzo et al. 2011). Esto determina una de las características más conspicuas de esta formación: la fenología distintiva de las plantas ligada a la pérdida estacional de las hojas y del bosque en general con una época sin hojas durante la estación seca y una fisionomía de bosque siempre verde a lo largo de la estación lluviosa. La densidad del estrato arbóreo, su diversidad y la continuidad del dosel arbóreo se va perdiendo a medida que el periodo seco se va extendiendo hasta dar paso a lo que se conoce como drylands o tierras secas (Maestre et al. 2011). En el extremo climático opuesto el bosque da paso a selvas siempre verdes cuando la disponibilidad de agua se extiende a lo largo de periodos más largos del año y las lluvias totales superan los 1600 mm (Murphy y Lugo 1995).

Los BTES ocupan el 42% de la superficie del bioma de bosque tropical (Miles et al. 2006). Sorprendentemente, a pesar de esta considerable extensión y del hecho de que estos ecosistemas soportan una importante población humana, los bosques secos del Neotrópico han recibido poca atención científica en comparación a los bosques lluviosos tropicales (Bullock et al. 1995, Sanchez-Azofeifa et al. 2005). Según Gentry (1995), el bajo interés en los BTES se debe a su baja diversidad, entre 50 y 70 especies con diámetro mayor de 2.5 cm en 0.1ha, en comparación con los Bosques húmedos, entre 200 y 250 especies mayores a 2cm de diámetro en áreas similares. Sin embargo,

esta tendencia ha cambiado durante los últimos años gracias al reconocimiento de que los BTES son uno de los ecosistemas tropicales más amenazados del mundo, menos conocidos al tiempo que dan cobijo a un alto porcentaje de poblaciones humanas que dependen directamente de los servicios ecosistémicos que ofrecen (Janzen 1988, Dinerstein et al. 1995).

El incremento de la investigación sobre los BTES, y especialmente sobre diferentes aspectos relacionados con la vegetación, durante la última década ha significado pasar de 2 artículos en el periodo 1990 a 1995 a 44 artículos durante el periodo 2006-2010 (Fig. 1.A). A pesar de este importante incremento en la investigación, éste no ha sido homogéneo en todos los países del Neotrópico donde este ecosistema es importante. Así, frente a la gran producción científica relacionada con los BTES en países como México y Brasil (50% del total producido en las regiones neotropicales) (Fig. 1.B), llama la atención el bajísimo número de publicaciones que han recibido los bosques interandinos de Ecuador y Perú así como los bosques de la Costa Pacífica de estos países.

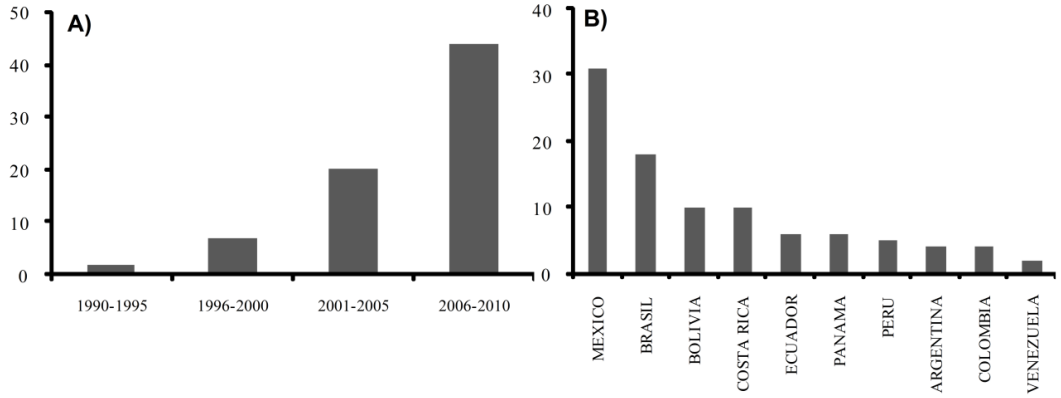

Figura 1. Desarrollo de la investigación sobre vegetación en los BTES desde 1990 mostrado como la producción científica de artículos en revistas recogidas en el ISI Web of Knowledge ("Dry-Forest" como topic y "vegetation" como filtro y considerando sólo los países del Neotrópico). A) Distribución de los artículos en periodos de 5 años, B) Distribución de artículos por país.

A pesar de los importantes avances en el conocimiento florístico de los BTES, el funcionamiento de estos ecosistemas es poco conocido, y cuestiones tan elementales como las respuestas de la comunidad vegetal a la estacionalidad y las variaciones de la

estructura de la comunidad frente a condicionantes ambientales y las perturbaciones, especialmente las de origen antrópico son poco conocidas.

Características de los bosques tropicales estacionalmente secos en el neotrópico

Diversos estudios han permitido establecer que los BTES durante las etapas glaciales más fría y secas conformaron un bioma más extendido de lo que en la actualidad se observa en el Neotrópico, de manera que la distribución actual de los BTES solo sería un remanente de este extenso bioma. (Prado y Gibbs 1993, Pennington et al. 2000).

Hoy en día los BTES aparecen de forma discontinua, en áreas de diferentes tamaño y con diferentes niveles de aislamiento extendiéndose desde el noroeste de México hasta el norte de Argentina y sureste de Brasil (Dirzo et al. 2011) (**Fig. 2**). Aunque los BTES son bosques más ricos que los bosques de latitudes templadas, como ya hemos comentado florísticamente son mucho más pobres que los bosques tropicales húmedos (Mayle 2004). La mayor parte de familias de plantas de los BTES aparecen bien representadas en el bosque tropical lluvioso aunque tres familias son únicas de los BTES neotropicales (*Zygophyllaceae*, *Canellaceae* y *Julianaceae*) y tres familias están mejor representadas en los BTES que en el bosque tropical lluvioso (*Capparidaceae*, *Cactaceae* y *Erythroxylaceae*) (Mayle, 2004). La familia dominante en la mayoría de los bosques estudiados en muy diferentes regiones es la de las *Fabaceae*, representada por un gran número de géneros y especies, y siempre con abundancias muy elevadas (Linares-Palomino y Ponce Alvarez 2005, Pérez-García et al. 2010, Linares-Palomino et al. 2010, Meira Arruda et al. 2011)

Los BTES tienen una mayor abundancia de especies espinosas (Pennington et al. 2000) y una cantidad de epifitas significativamente menor (ej. 10 individuos/0.1ha en Capeira, Ecuador) que el bosque lluvioso (ej. 4517 individuos/0.1ha en Rio Palenque, Ecuador) (Gentry 1995) (Mayle, 2004). En términos de estructura dasométrica, presentan menor área basal y altura de los árboles (Murphy y Lugo 1986). Esto es sin duda consecuencia de una caída de la producción primaria neta asociada al mayor estrés hídrico al que se ven sometidas estas comunidades. Lógicamente la actividad biológica queda fuertemente restringida por la disponibilidad de agua por lo que en época lluviosa es

cuando se manifiesta toda su potencialidad productiva (Murphy y Lugo 1986, Pennington et al. 2000, Mayle 2004). Otro atributo muy característico de estos bosques es que durante la época seca se produce una acumulación de hojarasca muy importante que tarda en descomponerse hasta la llegada de la época de lluvias debido a la baja humedad durante el resto del año (Pennington et al. 2000).

A grandes rasgos, los BTES neotropicales pueden clasificarse en tres grandes grupos (**Fig. 2**): i) bosque seco con dosel continuo, ii) sabanas (Furley et al., 1992) y iii) el Chaco (Prado y Gibbs 1993). Se ha sugerido que las diferencias entre estos ecosistemas están relacionadas con el grado de fertilidad del suelo y su pH, en el caso de los dos primeros, y de las condiciones climáticas en el caso del Chaco. El bosque seco *sensu stricto* requiere suelos más ricos y fértiles, mientras que las sabanas están restringidas a suelos ácidos con baja disponibilidad de calcio y magnesio y generalmente alta concentración de aluminio (Furley y Ratter 1988). Las sabanas normalmente se presentan en hábitats con suelos poco profundos donde el fuego es un factor de perturbación frecuente (Pérez-García et al. 2010, Pausas y Bradstock 2007). Finalmente los BTES ligados al Chaco aparecen a mayores latitudes, la vegetación de estos ecosistemas se encuentra sometida a una baja humedad del suelo e incluso a congelación en la estación seca que ocurre durante el invierno, mientras que en la estación húmeda sufre anegamiento y temperaturas que llegan hasta 49°C (Pennington et al. 2004, López et al. 2006).

Pennington et al. (2000) afina algo más esta clasificación inicial y plantea una subdivisión geográfica de estos sistemas tres tipos básicos de BTES. El bosque seco se encontraría según este autor representado por 9 núcleos biogeográficos distintos (Ver Fig. 2): 1) la Catinga brasileña, 2) Misiones en Paraguay y Brasil, 3) el Piedemonte andino desde Argentina hasta el norte de los BTES Bolivianos, 4) valles interandinos del norte de Perú, Bolivia y Ecuador, 5) costa del Pacífico de Ecuador y Perú, 6) valles interandinos de Colombia y Venezuela, 7) costa del Caribe de Colombia y Venezuela, 8) México y América Central, 9) islas del Caribe. Por otro lado las sabanas se encontrarían representadas por dos núcleos; 1) el Cerrado brasileño y 2) los Llanos venezolanos. Por último para el Chaco mantiene sólo un gran núcleo.

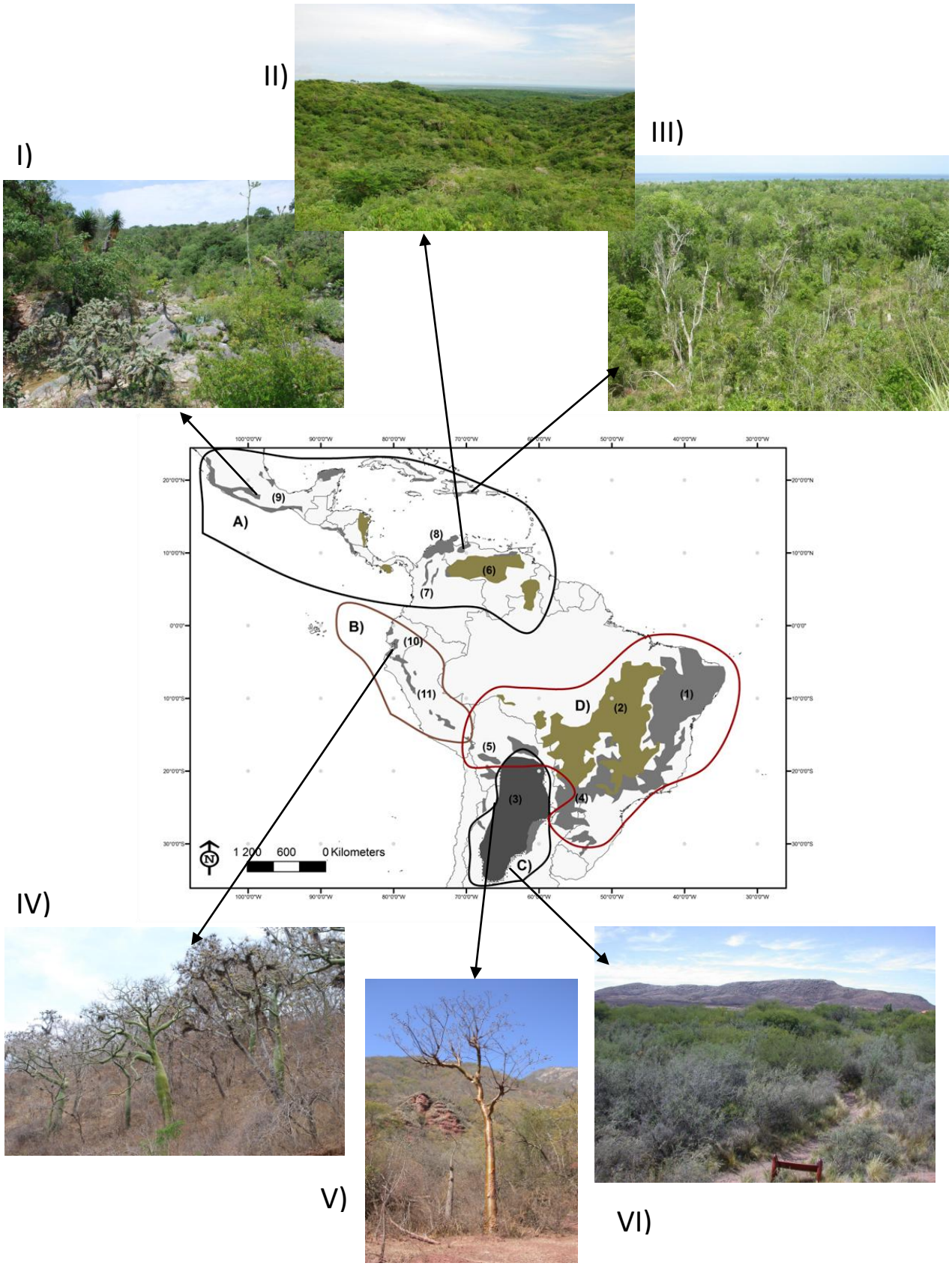

Figura 2. Distribución de núcleos de Bosque Tropical Estacionalmente Seco (BTES) en el Neotrópico. Los colores de los núcleos representan los tres tipos de vegetación de los

BTES; gris obscuro el Chaco, gris los bosques secos y oliva las sabanas. Los polígonos muestran los grupos florísticos biogeográficos; A) Mesoamérica y el Caribe, B) Costa del Pacífico, C) el Chaco, D) la Catinga. Los principales núcleos de BTES; 1) la Catinga, 2) Cerrado, 3) el Chaco, 4) Misiones, 5) Pie de Monte, 6) los Llanos venezolanos, 7) valles interandinos de Colombia y Venezuela, 8) Costa del Caribe y Venezuela, 9) México, 10) costa del Pacífico de Ecuador y Perú, 11) valles interandinos del norte de Perú, Bolivia y Ecuador. Basado en Linarez-Palomino et al. 2011. Las fotos muestran ejemplos de algunos ecosistemas de los BTES; I) Matorral seco San Luis Potosi, II) Matorral seco Venezuela, III) Bosque seco República Dominicana, IV) Bosque seco Pacífico Ecuatorial, Ecuador, V) Bosque Chaqueño, Argentina, VI) Caldenar, Argentina

Patrones de diversidad y endemismo

Se han llevado a cabo algunos intentos de describir los patrones de diversidad en el Neotrópico (Gentry 1995, Linares-Palomino et al. 2011). Así, Gentry (1995) señala la existencia de una tendencia latitudinal opuesta a lo observado en los bosques tropicales húmedos, con una baja diversidad en el ecuador que se incrementa conforme nos alejamos a latitudes más altas. En el ecuador muchas de las familias y géneros habituales están pobremente representadas, lo que posiblemente sea una de las razones de la baja diversidad observada en estas latitudes (Linares-Palomino et al. 2011). Por otro lado, aunque parece existir una tendencia general y clara en el sentido de incrementar la diversidad con la precipitación lo cual explicaría por qué en los BTES hay una menor diversidad que en los bosques lluviosos, éste no parece ser un factor que permita explicar por si solo los cambios de diversidad dentro de los bosques secos (Gentry 1995, Espinosa et al.2011).

La diversidad de los núcleos biogeográficos propuestos por Pennington et al. (2000) es muy variable: hay núcleos con baja diversidad como los Llanos en Venezuela o los valles interandinos de Bolivia que acumulan respectivamente tan solo el 1.17% y 1.59% del total de las especies reportadas para los BTES del neotrópico. Otros núcleos como los de la Catinga y Misiones albergan respectivamente el 30.86% y 41.73% del total de especies del ecosistema (Linares-Palomino et al. 2011). Las diferencias también son

importantes cuando se analiza el porcentaje de especies endémicas de cada núcleo, que varía desde el 7.8% en la Catinga hasta el 77.5% en las islas del Caribe (Linares-Palomino et al. 2010). Esta información, sin embargo, debería ser tomada con precaución debido a que esta comparación se basa en información obtenida con esfuerzos de muestreo notablemente diferentes, así mientras algunos núcleos están bien estudiados como los de la Catinga en Brasil, existen algunos pobremente estudiados como el núcleo de los valles interandinos del norte del Perú para el cual no hay prácticamente información.

Aunque tal como hemos detallado los núcleos biogeográficos establecidos por Pennington et al. (2000) poseen características estructurales y florísticas propias, se pueden encontrar afinidades entre núcleos que indican fuertes relaciones históricas y biogeográficas entre regiones. Los análisis florísticos llevados a cabo por este autor muestran la conformación de cuatro grandes grupos entre todos los núcleos conocidos (fig. 2). El primer grupo *Mesoamérica y el Caribe* que lo conforman los núcleos de la costa del Caribe de Colombia y Venezuela, los Llanos venezolanos, México y América Central que han mostrado ser una unidad biogeográfica consistente en otros trabajos (Gentry 1982, Linares-Palomino et al. 2011). Este grupo está caracterizado por la alta diversidad de sus núcleos, además por poseer los porcentajes más altos de endemicidad (Santiago-Valentin y Olmstead 2004). El siguiente grupo *Costa del Pacifico* que está conformado por los núcleos denominados valles interandinos de Perú, Bolivia y Ecuador, y costa del Pacífico de Ecuador y Perú. Este segundo grupo se encuentra separado del primero por la zona biogeográfica de selvas húmedas del Chocó, que constituye una barrera para las especies de climas más secos situados al norte (Best y Kessler 1995, Gentry 1995). Este grupo se corresponde con lo que se ha denominado región Tumbesina (Best y Kessler 1995) y se constituye como uno de los grupos de BTES neotropicales con mayor aislamiento, lo que ha originado una alta concentración de especies endémicas. Según los datos de Linares-Palomino (2011) esta zona es la segunda en concentración de endemismos de plantas de los BTES después de las islas del Caribe pese a que la diversidad total es más baja que en otras zonas; además es unas de las zonas con mayor biodiversidad y concentración de endemismos de aves (Best y Kessler 1995) lo que refuerza la originalidad del territorio. Desafortunadamente también esta zona permanece muy poco estudiada. El tercer grupo está conformado por el

Chaco. Es uno de los que presenta mayor extensión geográfica aunque en extensas áreas y podría ser clasificado como un matorral espinoso, con una densidad relativa mayor a la de los bosques secos debido al menor tamaño de los arbustos (Gentry 1995). Este grupo presenta una gran diferencia florística con el resto. Aparentemente, tal como ya hemos comentado, estas diferencias se deben a las peculiares condiciones climáticas (temperaturas más frías) en su área de distribución y a una mayor amplitud térmica a lo largo del año (López et al. 2006). Finalmente, el último grupo lo conforman la *Catinga*, los bosques secos de Misiones, el denominado Piedemonte (incluyendo el norte de los BTES bolivianos) y el Cerrado. Estas últimas zonas son las más diversas, sin embargo el grado de endemicidad de cada una de ellas es relativamente bajo, situándose entre el 14.8 y el 1.9% respectivamente (Linares-Palomino et al. 2011)

Estructura y funcionamiento de la vegetación de los BTES

Los avances realizados durante estos últimos años han permitido entender algunos de los procesos que participan en la estructuración de las comunidades vegetales en estos ecosistemas. La disponibilidad de agua sin lugar a dudas es uno de los factores limitantes más importantes en los BTES, siendo crítica para el establecimiento, supervivencia y desarrollo de las plantas (Ruthemberg 1980), condicionando tanto los gradientes espaciales (Balvanera et al. 2011, Espinosa et al. 2011), los procesos ecológicos básicos y las interacciones bióticas que se establecen en cada bosque (Martinez-Yrizar et al. 1992, Mooney et al. 1993). Además de la disponibilidad absoluta, la estacionalidad y la variación interanual de la precipitación marcan la dinámica de las comunidades vegetales y la estructura florística en los BTES (Blain y Kellman 1991, Murphy y Lugo 1995, Sampaio 1995).

Los BTES reciben alrededor del 80% de la precipitación durante 5 meses. A lo largo de estos meses la media de precipitación puede sobrepasar con creces los 100 mm por mes (Maass y Burgos 2011). En el otro extremo, durante los meses secos la precipitación raramente supera los 10 mm mensuales (Maass y Burgos 2011), creando un déficit hídrico que causa la pérdida de hojas de la mayoría de especies (Gotsch et al. 2010, Lima y Rodal 2010). Esta variación de meses lluviosos *versuss* meses secos es una constante en los BTES, sin embargo, superpuesta a esta fuerte variación estacional

existe una elevada variación interanual ocasionada entre otros por la acción de los fenómenos ENSO (El-Niño Southern Oscillation) y la corriente de California en mesoamérica (Best y Kessler 1995).

El reclutamiento y la regeneración en los BTES

El reclutamiento de plantas en el bosque seco está mediado como en otros sistemas forestales por la interacción entre factores bióticos y abióticos (Powers et al. 2009). Dichos factores afectan a dos procesos críticos para la regeneración: i) la producción de estructuras de regeneración (semillas, propágulos vegetativos y/o rebrotes), y ii) el establecimiento de estos propágulos o rebrotes.

Parece estar aceptado que en estos bosques la importancia relativa de semillas y rebrotes en el reclutamiento depende de las condiciones climáticas. La regeneración por rebrote, que estrictamente son "ramets" de genotipo idéntico al individuo "parental" (Ceccon et al. 2006), en muchas especies de árboles y arbustos es más importante que la regeneración por semillas (Murphy y Lugo 1986, Kauffman 1991, Rico-Gray y García-Franco 1992, Swaine 1992, Miller y Kauffman 1998). En sistemas tan estresantes climáticamente como el de los BTES este tipo de regeneración es favorecido, dado que el desarrollo a partir de brotes vegetativos puede aprovechar el extenso sistema de raíces y el almacenamiento de nutrientes en las partes restantes de la planta madre especialmente inmediatamente después de cualquier tipo de perturbación (Koop 1987, Negrelle 1995). Obviamente, las plántulas generadas a partir de semilla suelen ser mucho más numerosas, sin embargo suelen tienen tasas de supervivencia menores que las de los rebrotes. Esto implica que una parte importante de los individuos recién reclutados a la comunidad se originan por rebrotes (Ceccon et al. 2004). Un dato que llama la atención y que podría estar relacionado con la importancia del reclutamiento por rebrote es que el banco de semillas es menos importante que en otros sistemas "próximos" ecológicamente como los de climas semiáridos (Rico-Gray y García-Franco 1992, Skoglund 1992, Miller y Kauffman 1998). La menor importancia de los bancos de semillas en los BTES está relacionada con la rapidez con la que las semillas pierden su viabilidad, que ha llevado a muchas especies a basar su estrategia regenerativa en el desarrollo vegetativo y a otras especies a desarrollar semillas

recalcitrantes, sumada a una alta mortandad de semillas por depredación o por mortalidad debida a patógenos (Ray y Brown 1994). Por otro lado, normalmente las semillas germinan rápidamente al llegar al suelo para minimizar estos riesgos de pérdida (Skoglund 1992). Aparentemente, este comportamiento es una respuesta evolutiva a la existencia de periodos cortos de condiciones benignas y bastante predecibles (Ceccon et al. 2006).

La supervivencia de las plántulas está fuertemente ligada al estrés hídrico (Ceccon et al. 2004), es por esta razón que la mayor parte de la germinación se da durante la época lluviosa. Por otro lado, los pulsos de precipitaciones extraordinarias originados por las variaciones interanuales dan como resultado picos de reclutamiento de especies durante años más lluviosos, mientras que en los años más secos el reclutamiento queda fuertemente restringido siendo mucho más importante la regeneración por rebrote durante dichos periodos (Ruthemberg 1980).

Otros factores que influyen en la producción de semillas, rebrotes y en la supervivencia de las plántulas como la competencia planta-planta y la disponibilidad de recursos a escalas espaciales pequeñas, pero relevantes para las plantas han sido menos estudiados. Sin embargo, algunos estudios muestran que las lianas influyen en la dinámica de los bosque secos reduciendo la fecundidad e incrementando la mortalidad de árboles (Schnitzer y Bongers 2002).

Factores que afectan a la distribución de la vegetación en los BTES

Los patrones espaciales y los mecanismos potenciales asociados a los patrones no-aleatorios de distribución de especies a escala pequeña han sido poco estudiados en los BTES (Balvanera et al. 2011). A dichas escalas se ha observado en varios casos que la disponibilidad de agua restringe los patrones de distribución de muchas especies y en consecuencia filtran las especies que forman la comunidad (Balvanera et al. 2011). A pesar de la existencia de esta correlación entre la distribución de especies y disponibilidad de agua, a escalas regionales muchos autores no han encontrado relaciones significativas entre la diversidad y la disponibilidad de agua en los BTES (Gentry 1995, Trejo y Dirzo 2002), y en algunos casos se ha encontrado una

correlación negativa, de manera que altos niveles de diversidad están asociados a sitios con mayor sequía (Espinosa et al. 2011). En este sentido la existencia de interacciones positivas planta-planta podrían estar incrementando la riqueza a nivel local en las zonas más secas.

Se ha demostrado también la existencia de gradientes altitudinales de diversidad a escalas regionales (Trejo y Dirzo 2002, Espinosa et al. 2011). Dado que es habitual que la altitud esté correlacionada con otros factores ambientales como temperatura y productividad (Pausas y Austin 2001, Korner 2003), no resulta sencillo entender en todo su alcance esta relación. Se ha visto en algunos gradientes altitudinales que la sustitución de especies es más drástica de lo esperado y no gradual tal como se ha descrito en los ecosistemas de bosques húmedos (Rodal et al. 2008), lo cual sugiere que otros factores están controlando la estructura y composición florística a escalas locales en los BTES.

Varios estudios han mostrado la importancia de la variación topográfica en la distribución de plantas en los BTES (Balvanera y Aguirre 2006, Alvarez-Yepiz et al. 2008, Espinosa et al. 2011). Las variaciones topográficas juegan un papel fundamental en mantener la diversidad en los ecosistemas secos al generar diferentes hábitats que favorecen a distintas especies (Segura et al. 2003, White y Hood 2004). Los efectos de la topografía están asociados a la generación de heterogeneidad a pequeña escala ligada en última instancia a la disponibilidad de agua y nutrientes; así, las zonas con mayor pendiente poseen menor disponibilidad de agua y una capa de suelo menos profunda lo que permite explicar por qué a escalas locales la diversidad se reduce con el aumento de la pendiente (ej. Linares-Palomino et al. 2010, Espinosa et al. 2011). En cualquier caso es necesario indicar que los trabajos realizados se han restringido a la evaluación del efecto de la topografía, pero está poco claro qué factores asociados a ésta son los que realmente estarían provocando esta variación de la diversidad.

Conclusiones e implicaciones para la conservación

Aunque los análisis florísticos de todos estos bosques en el Neotrópico es incompleto resulta evidente que los BTES albergan una gran diversidad de especies vegetales (Lott

et al. 1987, Gentry 1995) y poseen una concentración de endemismos que se encuentra entre las más altas de los trópicos (Davis et al. 1997), sin embargo, la falta de información y el relativo escaso esfuerzo dedicado por la comunidad científica ha retrasado el conocimiento de mecanismos potencialmente implicados en el mantenimiento de esta diversidad (Balvanera et al. 2011). Hasta ahora se ha podido evidenciar cómo ciertos elementos abióticos estarían condicionando la distribución de las especies y generando patrones de riqueza a diferentes escalas espaciales, pero aún se conoce muy poco sobre la influencia que las interacciones bióticas tienen en la estructuración de la comunidad y en la organización de los ensambles de especies locales. Por otro lado, los procesos de regeneración y dinámica de estos bosques han sido también poco explorados lo cual resulta extraordinariamente llamativo si comparamos con lo mucho que se sabe sobre "drylands" y sobre bosques húmedos tropicales, las dos formaciones que flanquean ambientalmente los BTES. Este desconocimiento probablemente alcanza su máxima expresión en los BTES situados en las latitudes ecuatoriales y especialmente en los BTES ecuatoriano-peruanos.

Las variables topográficas juegan un papel importante en la generación de nichos que diversificarían los existentes y en alguna medida podrían ayudar a mantener los valores relativamente elevados de diversidad de los BTES. En este sentido, el efecto topográfico sería en realidad una respuesta a variaciones a pequeña escala en otras variables, como nutrientes o disponibilidad de agua entre otras, siendo necesario explorar mejor cómo estas variables afectan a la vegetación.

En el caso del Neotrópico, varios estudios (Janzen 1988, Best y Kessler 1995, López y Zambrana-Torrelio 2005, Fajardo et al. 2005, Miles et al. 2006) han permitido constatar el grave estado de conservación de los BTES como consecuencia de una alta presión antrópica y de la existencia de procesos de deforestación extremadamente acelerados. La pérdida de cobertura natural en los BTES a nivel mundial se encuentra situada alrededor del 48% para el área primitivamente ocupada por este ecosistema (Hoekstra et al. 2005), mientras que en algunos países del Neotrópico los valores totales podrían ser incluso mayores, en algunos núcleos podría alcanzar el 66 %, y lo que es más grave las tasas de deforestación anual podrían situarse entre 2 y 4.6% lo que condicionaría enormemente su persistencia en muchos lugares (Sanchez-Azofeifa y Portillo-Quintero

2011). El principal impulsor del cambio y la destrucción en los BTES es la expansión de la frontera agrícola, ya que en muchas ocasiones estos bosques están ubicados en áreas con excelentes suelos para la agricultura, y la expansión de la ganadería (Kalacska et al. 2005). Por otro lado, estos bosques poseen recursos madereros importantes lo que ha ocasionado la pérdida de cobertura de estos bosques y la desaparición de alguno de sus elementos florísticos más característicos (Sanchez et al. 2006, Sanchez-Azofeifa y Portillo-Quintero 2011)

Como se puede evidenciar la situación de los bosques tropicales estacionalmente secos es preocupante, debido al bajo conocimiento que tenemos de su funcionamiento así como a sus severos problemas de conservación. Un problema añadido tiene que ver con la escasa percepción de valor que para las comunidades locales tienen estos bosques. Como consecuencia de ello los BTES están muy poco representados dentro de los sistemas de conservación estatales de los países neotropicales, lo cual aumenta el riesgo de pérdida y no garantiza la conservación de esta diversidad y "complejidad". Es por ello que muchos de los países neotropicales han definido como una prioridad de conservación a los bosques secos.

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CAPÍTULO 2: WHAT FACTORS AFFECT DIVERSITY AND SPECIES COMPOSITION OF ENDANGERED TUMBESIAN DRY FORESTS IN SOUTHERN ECUADOR?

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Abbreviations

CCA: Canonical Corresponce Analysis; DBH: Diameter at Breast Height; GLM: Generalized Linear Models; LINKTREE: Linkage Trees; SIMPER: Similarity Percentage procedure; SIMPROF: Similarity Profile permutation test.

Abstract

This paper reports a study on species richness and composition of Tumbesian dry forest communities. We intended to test two alternative hypotheses about species assemblage processes in tropical dry forests: 1) species assemblage was determined by the filtering effect of environmental conditions and 2) species assemblage was determined by facilitative processes along the gradient of water availability, and thus, species richness and evenness would increase as water becomes limited. In addition we also explored the effect of climate and soil conditions on species composition in tropical dry forests. Species composition was sampled in 109 plots in terms of cover and tree diameter at breast height. Climatic, edaphic, topographic and anthropogenic degradation variables were obtained for each plot. We used generalized linear models and canonical

correspondence analyses to evaluate of effect environmental variables in species composition and richness and evenness. Water availability negatively affected richness and significantly determined the species assemblage. Species richness increased from ridges to valleys and evenness increased at higher altitudes. Soil characteristics showed no effect on richness and evenness but soil moisture, nitrogen concentration and soil temperature explained significant fractions of species composition. Although timber extraction and livestock in our study area was of low intensity it negatively affected richness but it had only a minor effect on species composition. Our results suggest that species composition in these endangered tropical dry forests may be at least partially explained by the stress gradient hypothesis, with higher species richness at drier conditions probably induced by facilitation processes.

Resumen

Presentamos un estudio sobre la riqueza y la composición de las comunidades del bosque seco Tumbesino. Probamos dos hipótesis sobre el ensamble de especies en los bosques secos tropicales: 1) el ensamble es determinado por el efecto de filtrado de las condiciones ambientales, los sitios más benignos serían más ricos en especies, y 2) la agrupación de especies es determinada por los procesos de facilitación en el gradiente de disponibilidad de agua (Hipótesis de la Gradiente de Estrés). Además, se exploró el efecto del clima y condiciones del suelo sobre la composición de especies en estos bosques. La composición de especies fue muestreada en términos de densidad y diámetro del árbol a la altura del pecho en 109 parcelas. Para cada parcela obtuvimos variables climáticas, edáficas, topográficas y de degradación antropogénica. Utilizamos análisis multivariantes para evaluar el efecto de las condiciones ambientales sobre la composición de especies y sobre la riqueza y equitatividad. La disponibilidad de agua afectó negativamente a la riqueza y determinó de manera significativa el ensamble de especies. La riqueza se incrementó de las crestas a los valles y la equitatividad fue mayor a mayor altitud. La humedad del suelo, la concentración de nitrógeno y la temperatura del suelo explicaron fracciones significativas de la composición de especies. Nuestros resultados sugieren que la composición de especies en estos bosques puede ser, parcialmente explicada por la hipótesis de gradiente de estrés, con una mayor

riqueza de especies en las condiciones más secas, probablemente inducida por los procesos de facilitación.

Keywords:

Anthropogenic degradation; community diversity; environmental constraints; precipitation in the driest month; soil physic-chemical features, temperature in the warmest month; tropical dry forest; vegetation.

Introduction

Since the seminal work of Janzen (1988), tropical dry forests have been recognized as one of the most threatened habitats in the world. Nevertheless, neotropical dry forests are disappearing at an incredibly high rate and, they now occur in a tiny fraction of their historic range (Fajardo *et al*. 2005). Vanishing dry forests are reduced to small isolated remnants from Mexico to Argentina (Maass 1995) due to timber extraction, fuel wood extraction and grazing by cattle (Fajardo *et al.* 2005; Leal-Pinedo & Linares-Palomino 2005). Only some remnants of these dry forests -less than 38 %- are currently included in some category of protection (Miles *et al.* 2006). Despite evidence of extreme threats and that forest losses are quickly accumulating (Janzen 1988), neotropical dry forests receive far less attention than other types of more humid tropical forests (Miles *et al.* 2006). Tropical dry forests have smaller stature and lower basal area than tropical rain forests (Murphy & Lugo 1986), they are diverse both locally and regionally (Givnish 1999) and although less known, they are almost as diverse as tropical rain forests. Ecological processes are strongly seasonal, and net primary productivity is lower than in rain forests because growth only takes place during the wet season (Pennington *et al.* 2000).

This conservation scenario worsens in southern Ecuador. From Gentry (1977), Ecuadorian dry forests are included among the most threatened ecosystems in this megadiverse country. More recently, Sierra (1999) explicitly pointed out that dry forest of the Loja province at the southern tip of the country should be the first national conservation priority. These Ecuadorian dry forests are part of the poorly explored

Tumbesian region (Dinerstein *et al.* 1995) which is recognized as one of the most endangered hotspots in the world and probably one of the less known (Janzen 1988).

The Tumbesian region covers a narrow fringe of land between the Pacific Ocean and Los Andes range and comprises the Southwest tip of Ecuador and the Northwestern edge of Peru. The Tumbesian region embraces altitudes from sea-level to 2000 and occasionally to 3000 meters and it is extended over 87.000 km^2 (Best & Kessler 1995, Dinerstein *et al.* 1995). The most important ecosystem is the seasonal dry forest which is characterized by the so-called ceiba (*Ceiba trichistandra*) and their *Bombacaceae* relatives (Aguirre *et al* 2006). These forests are extremely species-rich and shelter an extraordinary assembly of narrow endemisms of very different taxonomic groups (Best & Kessler 1995). Unfortunately, they are currently not protected in Ecuador and and only a tiny portion of them are protected in Peru in Cerros de Amotape National Park.

Knowledge on diversity patterns and environmental filtering factors is essential for proper management and conservation purposes of neotropical dry forests (Sánchez-Azofeifa *et al.* 2005), especially in the case of declining tropical dry forests (Balvanera & Aguirre 2006). Even more, increasing our knowledge about how these dry forests vary in species composition and other community attributes and their responses to environmental changes, both natural and anthropogenic, is a priority (Aguirre *et al.* 2006). In order to unveil these relationships we should take into consideration that water availability is probably the main driver of species coexistence in these forests (Balvanera & Aguirre 2006). It is well known that variation in climate –rainfall, temperature and range of temperatures- together with some local factors such as slope, geologic substratum and soil features can control evapotranspiration and, consequently, reduce water availability in the field. This may create a local water availability gradient that would likely affect species composition and species richness by either of two ways: 1) water availability acting as a critical factor that filters those species able to survive 2) plant-plant interactions through competition and facilitation. Under lower water conditions it is expected that positive interactions will prevail (Stress Gradient Hypothesis, Bertness & Callaway 1994). This kind of interaction should favor plant recruitment out of the species optimum in more stressful low water conditions Relative importance of climate and local factors as drivers of community assemblages is a

central issue in ecology and biogeography (Hubbell 2001; Ricklefs 2004). While the high local species richness of tropical dry forests is well documented (Valencia *et al.* 2004; Sánchez-Azofeifa *et al.* 2005), factors that control local species composition at spatial scales important for conservation management are poorly known. Accordingly we sampled dry forests in southern Ecuador and tested how regional (climate) and local (soil features, topography and anthropogenic degradation) factors may be related to composition, and diversity attributes of Tumbesian dry forests. We also wanted to test our two alternative hypotheses explaining species richness in these forests: 1) These community traits are determined by environmental filtering so we expect more benign sites to be richer in species and 2) species assemblage was determined by plant-plant interactions along the gradient of water availability, and thus, species richness and evenness would increase towards the more stressful water conditions where facilitation should dominate, whereas in more wet sites, species are excluded by competitive exclusion. Even more, we described the different floristic forest communities and make an effort for connecting this diversity to easily measurable variables such as temperature, precipitation and altitude thresholds. In this sense, our working hypothesis is forest species composition should hierarchically reflect first, the effect of climate and second other local effects such as soil characteristics. In order to partial out the small but expectable anthropogenic effect on composition we also included this source of variation in our models.

This study will contribute to understand the biodiversity of this unknown and threatened megadiverse region, the role that environment heterogeneity play in shaping tree assemblages of dry Tumbesian forests and to generate base information for conservation management.

Methods

Studied area

Tumbesian dry forests cover a territory about 87,000 km^2 that spans from the Southwest tip of Ecuador to the Northwestern extreme of Peru (Dinerstein *et al.* 1995). Our study area comprised nearly 1,864 Km^2 in the province of Loja (Zapotillo, Macara and Celica

districts) in one of the largest and best conserved remnants of the Tumbesian dry forests (Aguirre & Kvist 2005). In all this vast territory, land management has been of low intensity during the last decades. We surveyed relatively well conserved stands that did not suffer deforestation, and with very little anthropogenic perturbation Average annual temperature in the region is around 24ºC and temperature ranges between 10 ºC to 33 ºC during the year. Mean annual precipitation is about 500 mm/year. The elevation range is between 120 and 2,640m asl.

These dry forests are the habitat of several endangered species such as: *Juglans neotropica* (Juglandaceae), *Siparuna eggersii* (Monimiaceae) both critically endangered (see Joergensen & León-Yánez 1999; Valencia *et al.* 2000)

Field work

We located 109 rectangular plots (10 x 50 m) on 48 forest stands in a stratified sampling design based on the available preliminary landscape maps in the zone (Cabrera et al. not published data) and with the aim to include the whole range of environmental conditions (Fig.S1). Two or three plots per forest stand were sampled. Plot size was chosen to be sure that they represent the diversity -richness and composition- of a typical dry forest in the region (see Balvanera & Aguirre, 2006). Total surveyed area was 5.45 ha. This sampling may not be efficient enough to explore processes occurring at smaller spatial scales like those related to fine soil heterogeneity which may critically affect recruitment processes, however, it is adequate for classification purposes, for testing some biogeographical hypotheses and mainly to generate basic information for conservation management. Altitude and slope of each plot was recorded with an altimeter and with a clinometer in a wooden rule of three meters located in the centre of the plot. Topographic location of each plot was measured on a semi-quantitative scale.

This topographic gradient was presumed to reflect a water availability gradient (ridge>hillside>valley). Within each rectangular plot, we identified the species and measured the diameter at breast height (DBH) of all individual trees and shrubs with diameter $\geq$ 5 cm. Soil was characterized by means of five soil cores of 5 cm in diameter and 5 cm deep, taken one in the centre, and four at the plot corners. We measured soil

temperature at 30 cm deep. Percentage of soil moisture was calculated by subtracting the dry weight to the water saturated weight of each sample. After taking this moisture value, the five subsamples were thoroughly merged before analyses in order to minimize soil heterogeneity at the plot scale. We measured percentage of total nitrogen content (Kjeldahl method), bulk density (g/cm^3) and pH. Although our study area was well conserved, we visually estimated anthropogenic degradation related to firewood and timber extraction and livestock. The anthropogenic degradation variable summarized presence and amount of stumps -which are good surrogates of selective logging intensity-, and evidences of cattle grazing activities in a semi-quantitative scale index: high, medium and low degradation.

Our regional scale predictors were related to climate. These variables were estimated with the Worldclim data base (Hijmans *et al.* 2005). Worldclim interpolated the climate variables to our 109 plots on the basis of the eight existing meteorological stations nearby the study area. This on-line tool estimates climate parameters derived from monthly values of temperature and rainfall of the latest 50 years. Selected climatic variables represented annual trends (annual temperature, annual precipitation) seasonality (annual temperature range and annual precipitation range) and extreme environmental factors (temperature of the coldest and the warmest months, and precipitation in the wettest and driest months). We detected high correlations and variation inflation factors -VIF- between many of these variables, so hereafter we only considered in our analyses four climatic variables that showed low level of correlation: annual precipitation, precipitation in the driest month, annual temperature range and maximum temperature in the warmest month.

Although some uncertainty has been reported especially of rainfall values in mountainous areas after using this interpolation tool (Hijmans *et al.* 2005), the values interpolated for our plots are reliable since the eight meteorological stations are regularly distributed throughout the study area and tropical dry forests are usually located in the foothills of the Andes.

Statistical analyses

Total species richness and evenness (Pielou 1966) were modeled by means of Generalized Linear Models (GLM, McCullagh & Nelder 1989). GLMs allow handling larger distribution types in addition to Gaussian distribution for the response variable than standard linear regressions. We applied a quasi-likelihood estimation of the regression coefficients because it allows estimating regression coefficients in data sets without fully knowing the error distribution of the response variable (Guisan *et al.* 2002). We built a saturated model with all 13 predictor variables (annual precipitation, precipitation in the driest month, annual range of temperature, maximum temperature in the warmest month, anthropogenic degradation, altitude, slope, topographic location, soil temperature, soil moisture, pH, total nitrogen content and bulk density). The significant terms of the model were identified using a forward stepwise approach (Guisan & Zimmerman 2000) and to avoid multiple comparison problems typical of forward stepwise analyses we fixed the threshold for significance in $p< 0.01$. Generalized Linear Models were built with S-PLUS statistical software (MathSoft 1999).

We built two main matrices (species per plot), one for density values (number of individuals of each species per plot) and the other for total plant basal area of each species (109 plots in rows and 102 species in columns). Detrended Correspondence Analysis (DCA) showed that axes lengths were above 3 standard deviation units in both main matrices and so Canonical Constrained Analyses (CCA) were performed (ter Braak 1986, Legendre & Anderson 1999). Our null hypothesis (H_0) was that the environmental variables did not exert any effect significantly different from random on species composition in terms of density and basal area of each species. Plant data were square-root transformed and down weighing of rare species was performed. Five constraining matrices were built. 1) The climate matrix included four variables: maximum temperature in the warmest month, annual temperature range, precipitation in the driest month and annual average precipitation. 2) The topography matrix was built with one continuous variable with values 1 for valley, 2 for hillside and 3 for ridge with represent decay in water availability. 3) The matrix with the intensity of degradation consisted in one vector coded as a continuous variable which values 1 for low degree of

degradation, 2 for medium and 3 for high degradation. 4) The soil matrix included five variables: soil temperature, soil moisture, total nitrogen content, pH and bulk density. Finally, 5) we built a complete environmental data matrix including all the above mentioned predictors, except for the "annual temperature range" variable that was eliminated from the complete data set due to the high VIF values. Thus, the complete matrix contained 12 variables. Total Variation Explained (TVE) by each constraining matrix was calculated as the sum of all canonical extracted axes (Borcard *et al*. 1992). Monte Carlo permutation tests were performed to determine the accuracy of the relationships (1,000 randomizations) between each pair of data sets (Legendre & Anderson 1999; ter Braak & Smilauer 2002). To reduce the number of explaining variables and to select the best predictors, we used a forward selection procedure; the selected variables were used to construct a reduced model. Partial CCAs were run for each of the constrained models in order to partial out the effect of each environmental matrix independently of the rest (Borcard *et al*. 1992). Partial CCAs with climate, soil and topography matrices were performed two by two and the intersection of the three matrices was calculated following the procedure used by Vincent *et al* (2006). All these analyses were performed with CANOCO for Windows v 4.5 (ter Braak & Smilauer 2002).

In order to build a classification of species assemblages, the species densities data set was subject to an agglomerative cluster analysis with complete linkage as the clustering algorithm. Data was fourth root transformed and the similarity matrix was built with the Bray Curtis distance among samples. (Clarke & Gorley 2006). This cluster analysis was tested by means of a Similarity Profile permutation test (SIMPROF procedure) and a Similarity Percentage analysis (SIMPER procedure) was performed in order to identify the species responsible for the floristic differences between groups in each node of the dendrogram, so maintaining the hierarchical structure of the classification. (Anderson *et al*. 2008). In order to identify the environmental variables that underlied this classification, we labelled each sample with the environmental variable thresholds obtained after a BIOENV analysis followed by a LINKTREE procedure. These analyses were undertaken with the PRIMER v.6. statistical programme (Clarke & Gorley 2006).

Results

Our results showed that the Tumbesian tropical dry forests had on average 625 individuals per ha (±294 S.D.) (DBH>5cm). Our 500 m^2 plots had on average 9.1 sp (± 3.6 S.D.) Mean DBH was 33.44 cm. We recorded 102 species (69 trees and 29 shrubs) in the 109 plots surveyed (see Appendix 1). Average values and ranges of each predictor in our study area is in Table 1. Three Bombacaceae species accounted for the 40.27% of the area at breast height (*Ceiba trychystandra*, *Cavanillesia platanifolia* and *Eriotheca ruizii*). The most abundant species were *Simira ecuadorensis* (Rubiaceae), *Tabebuia chrysantha* (Bignoniaceae) and *Eriotheca ruizii*, which appeared in more than the 40% of the plots. On the other hand most species (54%) appeared in less than the 5% of the plots. We also recorded seven enlisted endangered species: *Juglans neotropica* (Juglandaceae), *Siparuna eggersii* (Monimiaceae) both critically endangered, and *Oreopanax rosei* (Araliaceae), *Verbesina pentantha* (Asteraceae), *Cavanillesia platanifolia* (Bombacaceae), *Pradosia montana* (Sapotaceae), *Erythrina smithiana* (Fabaceae).

Species richness was negatively affected by annual temperature range, annual precipitation, anthropogenic degradation and topographic location (species richness increased from ridges to valley bottoms), whereas evenness showed a positive relationship with altitude only (Table 2). Species composition both in terms of densities or in terms of basal area showed similar patterns when they were constrained with any of the explaining matrices (Table S1). Climate, topography and soil data sets explained fractions of total variation ranging from the 12% to the 16%, whereas anthropogenic degradation only explained a low but significant fraction of species composition (below the 4%). Climate was the constraining matrix that explained the highest percentage of species composition variability after excluding the overlap with the rest of data sets, followed by soil physicochemical variables (Fig. 1). Climate, soil and topography matrices showed very slight overlap in the variation explained, and anthropogenic degradation became non significant after adjusting for the variability explained by the rest of environmental matrices. In the forward stepwise procedure for the densities and basal areas, nine and eight environmental variables were selected, respectively (Table 3). Variables related to water availability explained the largest fraction of variability in

species composition: i.e. altitude, precipitation in the driest month, annual precipitation, soil moisture and temperature in the warmest month.

	Average ± standard deviation	Range
Species richness	9.10 ± 3.7	1 to 19
Evenness	3.94±1.1	0 to 6.6
Slope (%)	17.31±12.9	0 to 45
Altitude (m)	604.71±284.1	200 to 1,580
pH	5.75±0.4	4.78 to 7
Organic matter (%)	4.51±2	0.03 to 13
Soil temperature (ºC)	25.84±3.4	19 to 34
Organic carbon (%)	2.65±1.2	0.04 to 7.55
Total nitrogen (%)	0.19±0.1	0.01 to 0.6
Soil bulk density (g/cm^3)	1.18±0.1	1.02 to 1.42
Soil moisture (%)	9.59±7.8	1.05 to 28.7
Temperature in warmest month (ºC)	30.98±1.4	27 to 32.9
Annual temperature range (ºC)	14.86±0.7	13.8 to 16.6
Precipitation in the driest month (ºC)	1.17±1.5	0 to 4
Annual precipitation (ºC)	746.51±253.2	270 to 1,284

Table 1. Range, average values and standard deviation of all the predictor and response variables measured in our study area.

Agglomerative cluster analyses and the corresponding permutation tests (SIMPROF procedure) classified our samples into seven groups in terms of taxonomic affiliation (Fig. 2). At each node the discriminating species between both groups were identified which gives an idea of the hierarchy underlying the classification (SIMPER procedure; Appendix 2). Thus, *Triplaris cumingiana* (Polygonaceae) and *Simira ecuadorensis* (Rubiaceae) were the species that discriminated between the two main groups of Tumbesian dry forests. In the two subsequent nodes the diagnostic species were *Myrcia fallax* (Myrtaceae) and *Styrax* sp. (Styraceaeae) in the first and *Simira ecuadorensis* and *Coccoloba ruiziana* (Polygonaceae) in the second node. Our seven floristic groups are also linked to conspicuous differences in altitude, annual precipitation and rainfall in the driest month (Fig. 2). Groups 1 and 2 were correlated to altitudes above 650 m being the water availability during the driest month higher for Group 2. In the range between 300 and 800 m we found samples from Groups 6 and 7 which differed in the annual average precipitation and precipitation in the driest month. Group 7 occurred in drier conditions than 6. Group 4 included samples occurring at altitudes ranging from 600 to 800 m and related to high precipitation values. In altitudes ranging from 200 to 590 m and in

absence of precipitation in the driest months two different groups were identified, Group 5 with higher mean annual precipitation values and Group 3 in drier conditions.

Discussion

Our results support only one of our hypothesis: Tumbesian dry forests have higher richness in sites with greater water stress, consitent with the interpretation that facilitation processes are important to structuring the plant communities. As expected our results showed that species richness and evenness were mainly affected by two factors underlining water availability: i) climate, as showed by the significant effect of some climatic predictors such as annual rainfall, precipitation of the driest month and annual range of temperature in both community traits ; and ii) altitude, in the case of evenness. Predictors related to water availability in areas with a marked seasonality in precipitation have already been associated with some components of diversity (Trejo 1998; White & Hood 2004). As a norm it has been suggested that availability of water increases productivity and consequently diversity (Dickson & Foster 2008). However our results are aligned with those of Gentry (1995) who suggested that this relationship does not occur in the dry tropics. In fact, our results showed that drier conditions increased richness which suggests that our plant-plant interaction hypothesis seem more plausible. Thus, the negative relationship between water availability and richness could be explained at least partially by the well-known stress-gradient hypothesis, a conceptual model predicting that the relative frequency of facilitation and competition will vary inversely across gradients of physical stress or ecosystem productivity (Bertness & Callaway 1994). In consequence, the number of species packed in more stresful conditions was higher than expected by chance whereas in more competitive conditions some species may competitively be excluded. In our study area the stress may be induced by water deficiency and nurse plant may improve their facilitative effect mainly by means of shade conditions on seedlings. Shadows caused by neighbors, improves water availability by decreasing the vapor pressure difference between the leaf of the beneficiary and ambient air. This occurs without a substantial resource cost to the benefactor (Brooker *et al.* 2008) and leads to higher diversity than in more competitive scenarios.

Variable	Coef.	Standard Error	*t* value	*p*	Resid Df	Resid Dev.	*F*	*P*	Cumul. D^2
Species richness									
Null					108	1,461.9			
Intercept	90.45	14.99	6.03	2.25E-08					
Ann. T. Ran	-4.24	0.92	-4.63	1.02E-05	107	1,015.9	62.66	**<0.0001**	0.3051
Anthr. Degr.	-1.48	0.42	-3.5	6.83E-04	106	919.44	13.55	**0.0004**	0.3710
Ann. Prec	-0.01	0.003	-3.82	2.19E-04	105	829.25	12.67	**0.0006**	0.4327
Topogr. Loc	-1.58	0.49	-3.19	1.83E-03	104	762.42	9.39	**0.0028**	0.4785
Evenness									
Null					108	124.54			
Intercept	3.69	0.41	9.036	6.66E-15					
Altitude	0.001	0.0004	3.063	2.76E-03	107	110.06	14.26	**0.0003**	0.1162

Table 2. The significantly selected variables after a forward stepwise procedure of the Generalized Linear Models (GLM) with 108 samples (1 outlier was eliminated). Two response variables: species richness and evenness. *Ann. T. Ran*: annual temperature range, *Anthr. Degr:* Anthropogenic degradation, *Ann. Prec*: Annual average precipitation, *Topogr. Loc*: topographic location, *T warm_m*: temperature of the warmest month, *Prec. dri-m*: precipitation of the driest month, *Soil T*: soil temperature. *Coef*: regression coefficient, *Resid Df*: residual degrees of freedom, *Resid Dev*: residual deviance, *F*: F-statistic, *Cumul.* D^2: cumulative D^2, (i.e. percentage of variance explained). The p threshold to select significant terms was $p< 0.01$ to avoid multiple comparison problems.

Surprisingly, species richness patterns in these tropical dry forest areas were not affected by soil characteristics. This result has to be taken with caution because it is well known that soil heterogeneity and ground surface variability are critical for the demography of some species but at finer spatial scales (Hook *et al.* 1991). However at the medium size scale we are working on, soil fine heterogeneity seems not to affect species richness, although species composition was affected.

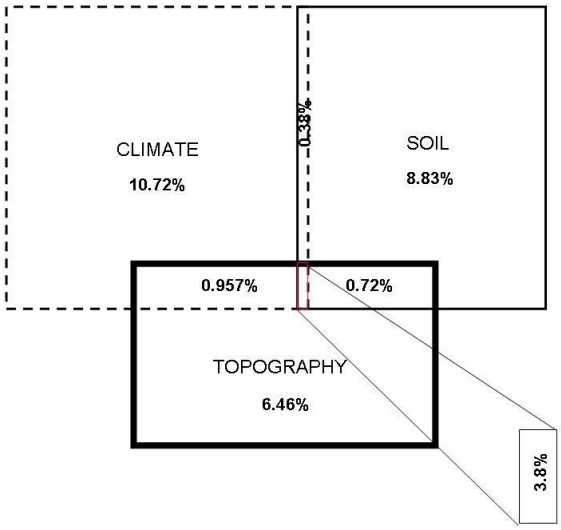

Figure 1. Variation in plant density explained by each of the constraining data matrices: Topography, Soil and Climate and the overlap of the variation explained among matrices after undertaking the partial CCA analyses (see the methods section). The effect of anthropogenic degradation became non significant after adjusting the rest matrices as covaribles in the partial CCA so it was not represented in this figure.

Some studies have shown that the effect of topographic location was commonly associated with diversity and also mediated by water availability (Oliveira-Filho *et al.* 1998). Species richness and evenness increased from ridges to valleys, first because probably at ridges environmental conditions are harsher (strong winds, shallower soils…) and these extreme environmental conditions may restrict the amount of species able to survive in these rough conditions, and second because rock outcrops at ridges may significantly reduce the available space for trees (Escudero 1996).

	Tree densities				**Plant basal area**		
Variable	**λ**	***F***	***p***	**Variable**	**λ**	***F***	***p***
Altitude	0.49	8.18	0.001	Altitude	0.47	6.83	0.001
Prec. dri-m	0.26	4.53	0.001	Prec. dri-m	0.26	3.79	0.001
Annual precip	0.23	4.09	0.001	Annual precip	0.25	3.71	0.001
Soil moisture	0.19	3.42	0.001	Nitrogen	0.16	2.58	0.001
T warm_m	0.15	2.92	0.001	Soil moisture	0.17	2.68	0.001
Nitrogen	0.13	2.42	0.001	T warm_m	0.15	2.28	0.001
Antrop_degr	0.13	2.42	0.001	Slope	0.12	1.94	0.001
Slope	0.12	2.32	0.001	Soil T	0.14	2.21	0.001
Soil T	0.12	2.35	0.001				

Table 3. Environmental variables selected in the forward stepwise selection in the CCA analysis on tree species densities and plant basal area (see Methods). *λ***:** variation

explained. *F*: F test statistic, *p*: significance (after Monte Carlo permutation test and Bonferroni adjustment). *Prec. dri-m*: precipitation of the driest month *Topogr. Loc*: topographic location, *Te warm_m*: temperature of the warmest month, *Antrop_degr*: Anthropogenic degradation, *Soil T*: Soil Temperature.

On the other hand total richness varied inversely along a human disturbance gradient. This is relevant since the intensity of disturbance in the sampled stands is low and we are currently assisting to a dramatic increase of this pressure especially in more accessible areas. Timber extraction and cattle grazing affected forest richness but not composition (see below). This suggests that extraction is not selective, so the number of species is maintained at least in this low pressure state.

Species composition of the Tumbesian dry forests was mainly determined by climate, topographic and soil. It is worth noting that densities and basal area data sets showed similar results. The climate data set explained the highest fraction of non overlapping information. Relevance of water was also highlighted because the selected climatic variables were also surrogates of this factor: temperature of the warmest month and rainfall of the driest month. Water availability has been recognized as one of the most important factors in determining species composition in tropical dry forests (Gentry 1995; White & Hood 2004). Soil predictors also played an important role in determining species composition in the line of other studies (Chytry *et al*. 2008). Soil variables related to water availability such as soil moisture and soil temperature were selected together with soil nitrogen concentration. Although soil features did not affect richness, it significantly controlled species composition, through surrogates of ecosystem productivity like nitrogen content. This implies that composition shifted in richer soils.

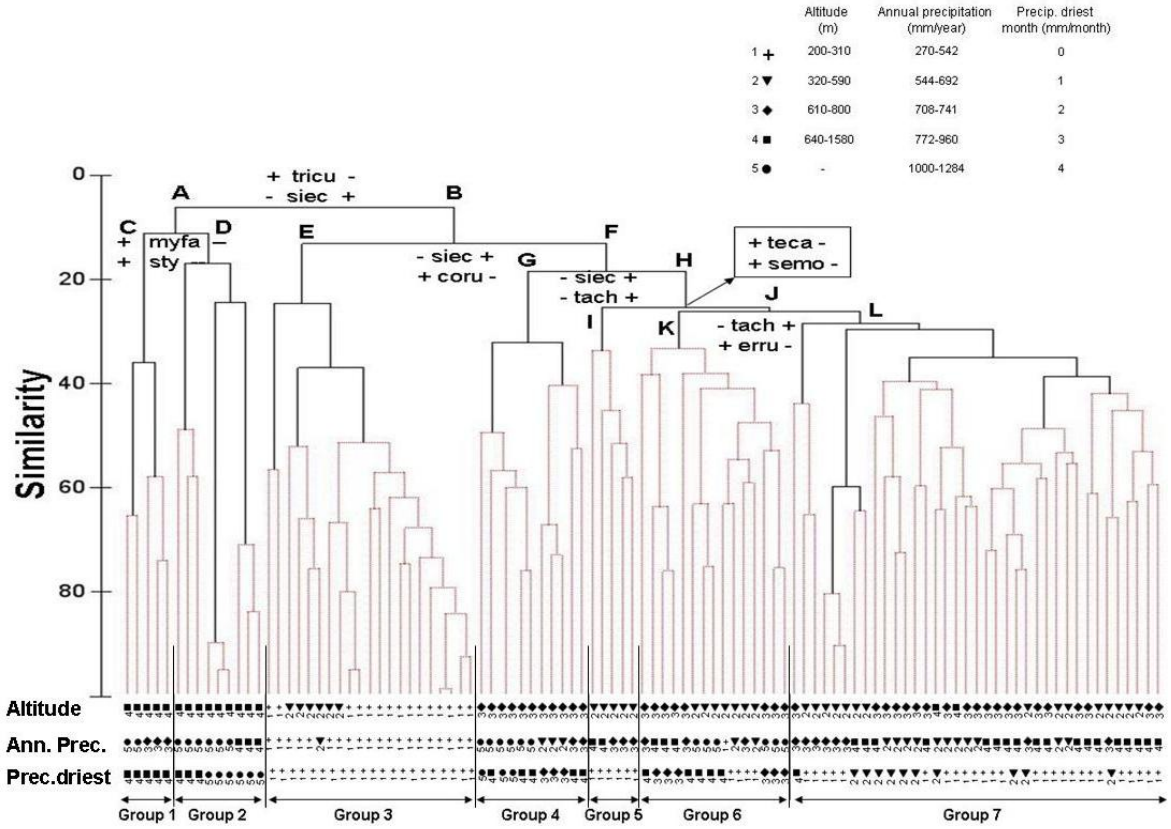

Figure 2. Dendrogram of the agglomerative cluster of 103 samples (6 outliers were excluded). Solid lines represent significant differences among groups by means of the permutation procedure SIMPROF. Data were fourth root transformed and the resemblance matrix was built by means of Bray Curtis distances. Species that contributed to the discrimination between groups are indicated in each node (SIMPER procedure). - and + symbols indicate in which groups the species were more abundant. Y-axis represents similarity percentage among groups. Capital letters indicate each node (for more details on SIMPER see Appendix 2). Ann. Prec.: Annual precipitation. Prec.driest: Precipitation in the driest month. Tricu: *Triplaris cumingiana*, siec: *Simira ecuadorensis*, myfa: *Myrcia fallax*, sty: *Styrax sp*, coru: *Coccoloba ruiziana*, teca*: Tecoma castanifolia*,semo: *Senna mollisima*, tach: *Tabebuia chrysantha*, erru: *Eriotheca ruizii*. The seven groups of samples obtained after de SIMPROF procedure, labelled with the environmental variables ranges identified in the LINKTREE analysis: altitude, annual precipitation and precipitation in the driest month.

Altitude was also a significant predictor of species composition of these dry forests (Aguirre *et al*. 2006). This result was probably related to the fact that at higher altitudes

the transition region between mountain and genuine dry forest communities appears. Several Andean species that have their lower distribution limits in our studied area appeared at higher altitudes (i.e. *Juglans neotropica* –Junglandaceae-, *Triplaris cumingiana* –Polygonaceae-, *Verbesina pentantha* –Asteraceae-, *Clusia sp*. –Clusiaceae-) implying an increase in diversity attributes typical of ecotones.

Our floristic classification in seven groups was in agreement with other floristic approaches carried out in this vast territory (Aguirre & Kvist 2005; Aguirre *et al.* 2006). For instance, the group dominated by *Myrcia falax* (Myrtaceae) and *Styrax sp.*, (Styracaceae) and the group dominated for *Simira ecuadorensis* (Rubiaceae) and *Tabebuia chrysantha* (Bignoniaceae), which appeared at the higher and medium altitudes of the tropical dry forest was almost coincident with a well-defined vegetation type by Aguirre & Kvist (2005). All these floristic groups were strongly segregated by altitude and water availability (Fig. 2).

In conclusion, the species assemblage in tropical dry forests seems to be controlled mainly by altitude (proximity to the Mountain Forest ecotone) and water availability. Reduction in water availability in the tropical dry forest generated communities with more species, probably in response to the stress, facilitation processes became dominant. Our results fill, at least partially part of the gap in the knowledge of dry forests ecology in South America (Sánchez-Azofeifa *et al.* 2005) and provide basic information for conservation management of poorly studied Tumbesian forests (Dinerstein *et al.* 1995, Aguirre *et al.* 2006).

Acknowledgments

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CAPÍTULO 3: SPECIES ASSOCIATION AND DIVERSITY STRUCTURE IN A TROPICAL DRY FOREST

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Abstract

Understanding how the high diversity is maintained in tropical ecosystems remains a challenge in ecology and has fostered the elaboration of multiple hypotheses to explain its maintenance. The neutral hypothesis proposed by Hubell predict that the diversity is maintain for stochastic process, however, many studies found that diversity is influenced by deterministic processes related to some ecological rules such as the abiotic filtering based on environmental heterogeneity and the plant-plant interaction.

One of the most efficient tools for explaining species coexistence and, for extension, for disentangling the prevalence of stochastic versus deterministic processes on plant community structure and composition is point pattern analyses. With this in mind, we used the Individual Species–Area Relationships (ISAR) to evaluate the species-specific effects on local taxonomic diversity (richness) in tropical dry forest in South of Ecuador.

Contrary to the neutral hypothesis proposed by Hubbell the results show that in these ecosystems, that support a high climate stress, the positive plant-plant relationships are an important way of maintaining diversity. The species in tropical dry forest show a low degree of clustering with its conspecifics as proposed by Janzen – Connell, which contributes the accumulator behavior of species. Interestingly, the behavior of the

species changes depending on their size, we observe that the large and small individuals operate independently of each other.

Introduction

Understanding how the high diversity is maintained in tropical ecosystems remains a challenge in ecology (Chesson 2000, Wright 2002) and has fostered the elaboration of multiple hypotheses to explain its maintenance (Janzen 1970, Connell et al. 1978, Hubbell et al. 1999, 2001, Chave et al. 2002, Giles et al. 2004, Volkov et al. 2005). For instance the so-called Neutral Theory proposed by Hubbel (2001) and recently revisited (Rosindell et al. 2011) predicts that stochastic immigration and mortality rule species coexistence at local scales, with the actual level of species richness determined by the size of the regional species pool, thus minimizing the influence of deterministic processes related to some ecological rules such as the abiotic filtering based on environmental heterogeneity and the plant-plant interaction in the community structure and composition. Although some works suggest the importance of ecological drift for structuring local communities (Rosindell et al. 2011) many evidences also show that the clumped distribution of species in these megadiverse tropical forests is compatible with the existence of plant–plant interaction (Wiegand et al. 2007b), differential responses to the small scale environmental heterogeneity (Ashton 1969, Grubb 1977), and also to the existence of negative density dependence (Janzen 1970, Connell et al. 1978).

One of the most efficient tools for explaining species coexistence and, for extension, for disentangling the prevalence of stochastic versus deterministic processes on plant community structure and composition is point pattern analyses (Wiegand et al. 2007b). It is especially suited to unveil the spatial component of the plant to plant interactions effects on population and community dynamics (Murrell et al. 2001, McIntire and Fajardo 2009). Interactions among plants and other sessile organisms are especially important for determining the neighborhood and usually extend over limited distances (Purves and Law 2002). Wiegand et al (2007a) proposed an original framework for evaluating the species–area relationships around individuals (ISAR-individual species area relationship-) which allows assessing the effects of individual species on the diversity of the whole community. The ISAR allows for a subtle assessment of species

effects on local diversity at multiple distances. This function can shed light on the interactions a species establishes with plants of other species. For instance if a species drives facilitative interactions, it will act as "diversity accumulator" and in its proximity we will find an over-representation of diversity. Contrarily a species is a "diversity repeller" when in its proximity we find less species than the number that could be expected from the global richness of the community; this effect could be a consequence of competitive interactions. Finally, the species are "neutral" when other species in its proximity are a random sample of the total floristic pool.

An initial study in two tropical forest plots: Barro Colorado Island (Panama) and Sinharaja (Sri Lanka) using the ISAR analysis has revealed that individual species have different effect on diversity spatial patterning and that the importance of repeller and accumulator behavior seems to be context dependent. The analyses revealed also that the two studied tropical forests lacked key species spatially structuring diversity, which is in accordance with Neutral Theory. However, under harsher environmental conditions a greater role of individual species in structuring local species diversity is expected due to the role played by facilitative interactions in these environments, where most species can ameliorate the environment for other species (Hacker and Gaines 1997, Wiegand et al. 2007a). This expectation implies that the number of accumulator species should be significantly higher under harsher conditions.

In order to test if an increase in stressful conditions implies an increase in the number of accumulator species at small spatial scales (facilitative interactions) in comparison with milder ecosystems we have computed the ISAR in a megadiverse tropical seasonal dry forest. Stress in these ecosystems is linked to seasonal water availability; the vegetation suffers from hydric deficit during eight months a year. This marked seasonality controls the dynamic and community structure of these forests (Blain and Kellman 1991, Murphy and Lugo 1995, Sampaio 1995). In stressful ecosystems such as this one, positive interactions play a key role in plant community structure (Bertness and Callaway 1994, Crain and Bertness 2006), i.e., the presence of some species able to modify the environment by reducing the frequency and intensity of some physical constraints, disturbance or stress, leads to ameliorate habitat conditions for less tolerant species and locally increase species diversity (Hacker and Gaines 1997).

The spatial structure and the potential mechanisms associated to non-random patterns in tropical dry forests has been little explored (Balvanera et al. 2011). The composition and spatial distribution of species in tropical dry forest seems to be associated to small scale (<1 ha) spatial heterogeneity of abiotic factors (Balvanera and Aguirre 2006, Balvanera et al. 2011) and it has been shown that the proportion of species with non-random distribution (72%, Balvanera et al. 2011) is greater than the fraction found in rain forests (60%) at comparable scales (Clark et al. 1999, Harms et al. 2001). Even in genuine rain forests small-scale soil heterogeneity has been shown to profoundly affect the spatial pattern of individual species (John et al. 2007) so if we want to evaluate the effects of biotic interactions in the spatial structure of the diversity it is necessary to take into account the environmental heterogeneity associated to such patterns which obviously is also spatially structured (Legendre and Legendre 1998).

We propose an evaluation of the species - specific influence in the spatial structure of the diversity –richness- and specifically testing the following hypothesis; i) the proportion of species that act as accumulators in tropical dry forests is higher due that this ecosystem supports stressful conditions ii) larger individuals generate conditions for the development of smaller individuals, thus the response in each size class will be different.

We used the Individual Species–Area Relationships (ISAR) (Wiegand et al. 2007a) to evaluate the species-specific effects on local taxonomic diversity (richness). More specifically we wanted to know the number of species occurring in average in the neighborhood of each individual of a species and at what distance. We need to measure the relationship between the spatial pattern of plants of the target species and the pattern of the plants of the other species of the community and compare it to a null model of a neutral species (Wiegand et al. 2007a).

Methods

Study Site

The study plot was located in the Ecological Reserve Arenillas (hereafter REMA). REMA is located at the southern tip of Ecuador in El Oro province, between the towns of Arenillas and Huaquillas and covers an area of 16958 ha with an altitude range from 0 to 300 m asl (Figure 1.A). Climate is characterized by a rainy season with an average annual precipitation in four months of 515 mm from January to April and 152 mm during eight months in the dry season. The mean temperature have a maximum variation of 3.4 ºC among the coldest and warmest months being the lowest temperature during the dry season (Figure 1B). REMA according to Sierra (1999) contains tree different types of vegetation; the dry scrub of lowlands, (0–50 m), the deciduous forest of lowlands (50–200 m) and the semideciduous forest of lowlands (100–300 m). These dry forests are considered the most endangered ecosystems in Ecuador (Gentry 1977, Sierra 1999) and constitute part of the Tumbesian biogeographical region. REMA shelters one of the last relict of dry forest in the Ecuadorian Pacific Coast where the dry forest remnants are almost extinct and remnants are heavily fragmented and degraded (Linares-Palomino et al. 2010).

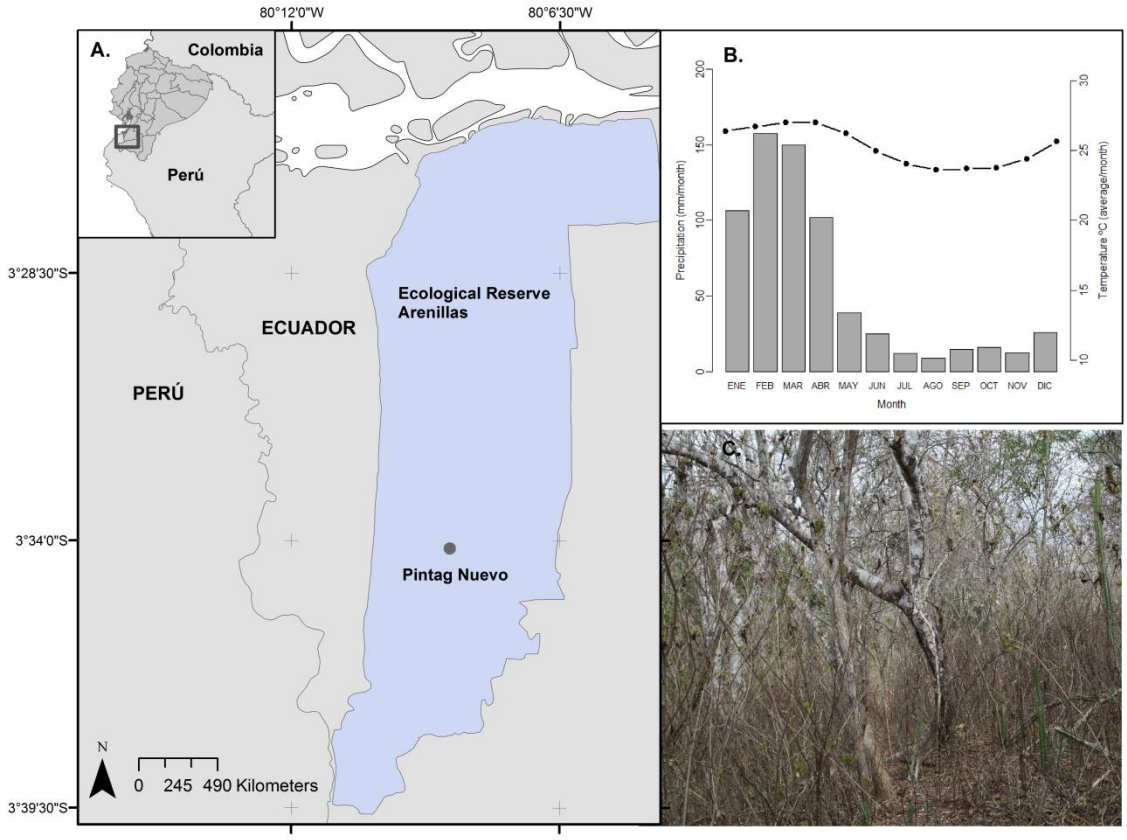

Figure 1. A. Location of ecological reserve Arenillas (REMA) in south of Ecuador. Grey circle show the study area near "Pintag Nuevo". B. Annual fluctuation of temperature and precipitation in REMA. C. Structure of the deciduous forest during the dry season.

In the center of REMA within a very well conserved area which is named "Pintag Nuevo" and covered by a transitional formation between deciduous forests and dry scrubs of lowlands we established a permanent plot. The most conspicuous tree species in the area are Bombacaceae and Bignoniaceae together with other families like Capparaceae and Euphorbiaceae which are more important in the dry scrub formation.

We delimited a 9 Ha (300 m x 300 m) square plot by locating on the field 225 subplots of 20 x 20 m (400 m2) each. During the rainy season (January and May 2010 and 2011) all the trees and scrubs with diameter at breast height above 5 cm were tagged, measured and identified to species. During the dry season (July and September 2010

and 2011) all the marked individuals were mapped using Leica total station, model TS02-5power with a precision below 5 cm.

To estimate spatial variability of local diversity throughout the permanent plot, we sampled the number of species in circles with 5, 10, 30 and 50-m radii placed on the nodes of a 4 x 4 m grid within an inner plot defined by trimming a margin of the same width as each radius off the whole plot.

Spatial pattern analysis

ISAR(r) is the expected number of species within circular areas with radius r around an average individual of a target species *t*. Following Wiegand et al. (2007a), we first calculated the bivariate emptiness probability P*tj*(0, r) that species j was not present in the circles with radius *r* around the trees of the target species *t* (without counting the focal stem if *t=j*) and then summed up 1-P*tj*(0, r) for all species (*N*) present in the plot. ISAR is then estimated as:

$$ISAR(r) = \sum_{j=1}^{N} [1 - P_{tj}(0, r)]$$

In order to evaluate whether the ISAR varies among size classes, i.e., if the size of individuals affect the interaction responses, we computed the ISAR for three sets of data: i) for all individuals larger than 5 cm of DBH, ii) for individuals larger than 10 cm of DBH and iii) for individuals between 5 and 10 cm of DBH. We computed also a "crossed" ISAR, using the larger individuals (> 10 cm DBH) of the target species and the small individuals (< 10 cm DBH) of the target and the other species as the individuals rendering the bivariate emptiness probability P*tj*; i.e., we are computing the expected number of species in the small individuals found within circular areas with radius *r* around an average larger individual.

With the purpose of explaining the behavior of each species (repeller, accumulator or neutral) we evaluated their relationship with some structural measures at two scales, i.e.,

within circles with radii 5 and 10 m. We selected these radii because we want to evaluate the effect of the target species on the grouping of species, avoiding the effects of habitat association. The measures employed were the total abundance of individuals in the plot, the clustering tendency of target species and the local dominance of target specie. As a measure of community evenness, we also calculated for each species and all radii the average Inverse Simpson Index.

The clustering tendency of target species is estimated as: $\Delta_{tt}(r) = M_{tt}(r) - \lambda_t a(r)$, where $M_{tt}(r)$ is the average number of stems of the target species within circles of the selected radius *r*; $a(r)$ is the circular area with radius *r* around the stems of the target species (not counting the focal stem) and λ_t is the intensity of the target species within the inner plot. $\Delta_{tt}(r)$ describes the tendency to clustering or regularity (if $\Delta_{tt}(r) > 0$, the species has a tendency to clustering and for $\Delta_{tt}(r) < 0$, the species has a tendency to regularity). The local dominance of the target species is defined as $D(r) = M_{tt}(r)/[M_{tt}(r) + M_{to}(r)]$, where $M_{to}(r)$ is average number of stems of all other species within circles with the selected radius *r* around the stems of the target species. The significance of these relationships was evaluated with Kruskal-Wallis tests.

Null models and statistical inference

We fitted heterogeneous Poisson models for each species in order to use them as null models for target species distribution. An heterogeneous Poisson model accounts for "first-order effects'' in the spatial distribution of individuals, i.e., spatial variation of intensity related to the (not measured) environmental heterogeneity and based on the fact that habitat association increases or decreases the likelihood that an individual will occur at a given location (Diggle 1983, Wiegand and A. Moloney 2004). For each species, we estimated the intensity function by using a Gaussian kernel with a bandwidth of 50 m. This bandwidth removes all potential spatial structure in the pattern of the target species at scales > 50 m, but maintains the spatial structure at scales <50 m, and was chosen based on several studies that have shown that direct plant-plant interactions occur at local scales than 20-30 m (Hubbell et al. 2001, Peters 2003, Uriarte et al. 2004, Stoll and Newbery 2005) and dispersal kernels in tropical forest typically range from 40 to 50 m (Wiegand et al. 2007a).

To assess deviations from the neutral behavior, we computed Monte Carlo simulation envelopes for each species based on the 99 simulations of the fitted heterogeneous null models. If the empirical ISAR(r) was at a given scale *r* larger than the second highest ISAR(r) of all 99 simulations of the null model, the species was regarded at scale *r* as a diversity accumulator with an approximate α level of 0.05. Conversely, if the empirical ISAR(r) was at a given scale *r* smaller than the second smallest ISAR(r) of all 99 simulations, the species was regarded at scale *r* as a diversity repellant. If the empirical ISAR(r) was within the range of the null model, the species was considered neutral at scale *r*.

Results

We mapped in total 4194 individuals with DBH greater than 5 cm, of these 2896 are trees, 909 are treelets and 389 are succulent. We found a total of 36 species with breast height diameter (DBH) greater than 5 cm, of these 20 species are trees, 15 species are treelets and 1 species is a succulent. The average abundance per hectare was 466 individuals; the trees were more abundant than treelets with 321 and 101 individuals per ha respectively. The abundance is more evenly distributed among trees since 90% of individuals belong to 11 species, being *Tabebuia billbergii* the most abundant specie, in the treelets the abundance is concentrated in 2 species which own 78% of the abundance of shrubs, *Cynophalla mollis* and *Croton sp.* are the most abundant arbustive species.

The mean and standard deviation of local diversity (species richness) in REMA was 2.8 ± 1.7 at 5 meters scale, 7.7 ± 2.5 at 10 meters, 19.8 ± 3.19 at 30 meters and 25.7 ± 2.8 at 50 meters. The distribution function of the number of species in the circular sampling areas with 5 and 10 m radii showed almost normal distributions, whereas at 30 and 50 m the distribution showed departures from normality (Figure 2).

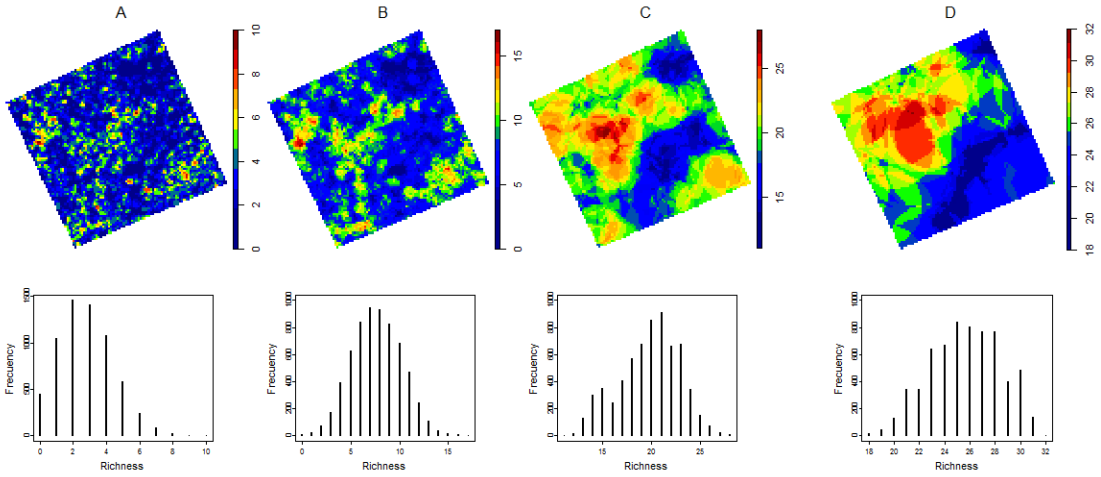

Figure 2. Variation in the spatial diversity in the dry forest of REMA at neighborhoods of 5, 10, 30 and 50 m (A, B, C, D respectively). In top show the spatial diversity variation and in bottom show the distribution function of the number of species in the circular sampling areas.

When considering all size classes together, most of the analyzed species behaved as neutral at practically all scales. However, at very short scales (1 and 2 m) accumulator species were predominant (around 50 %), and maintained percentages well over 20 % for almost all scales (Fig. 3A). The percentage of repellers was almost null at all scales. For the small size class (between 5 and 10 cm DBH), neutral behavior was again predominant but more than 30 % species were accumulator up to scales around 15 m and even at 7 m scale accumulator was the common behavior (50 %). For scales over 15 m we found around 15 % of accumulators. Repellers were again practically null (Fig. 3B).

Analyzing the larger class alone (DBH > 10 cm) showed that neutral behavior was predominant at all scales and that accumulators were abundant at scales between 13 and 15 m (around 40 %) and then decreased to around 15 %. In this case we found a 10 % of repellers at short scale (1 to 10 m).

The crossed ISAR showed that the effect of larger individuals in the spatial structure of small individuals was neutral for most species and that this behavior was predominant at all scales. Some species (around 22%) behaved as accumulator between 13 and 27 m

were as around a 10 % acted as repellers at 14 m and increased to 18% at 26 m; this proportion remained up to 47 m.

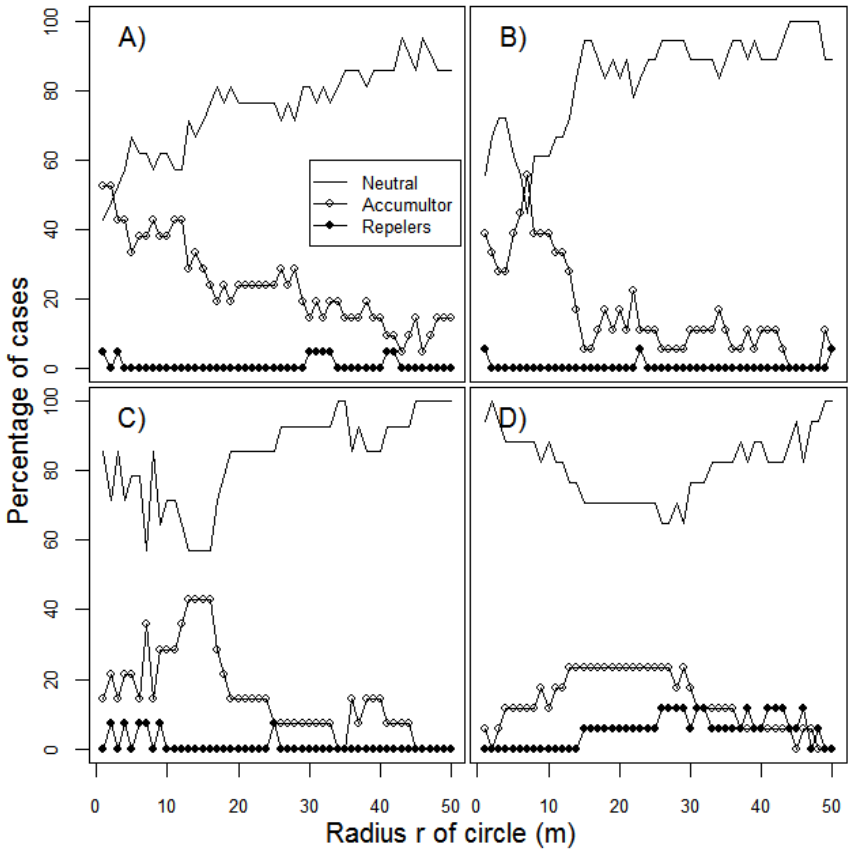

Figure 3: Proportion of significant diversity accumulators and repellers at REMA. A) All size classes analyzed together, B) Only small (<10 cm DBH) individuals C) Only large (>10 cm DBH) individuals, D) Crossed ISAR: proportion of species with large trees behaving as significant accumulator or repellers of small individuals diversity.

Of the 21 targeted species none behaved as repeller at the 5 and 10 m scales. The Kruskal Wallis test did not find any significant relationship between the behavior of each species (neutral or accumulator) and their abundance, local dominance [$D(r)$] or clustering tendency [$\Delta_{tt}(r)$], at the evaluated scales of 5 and 10 m. The behaviour of the individual species was not directly related to their abundance at 5m and 10m. The abundance of accumulator species was variable ranging from fewer than 100 individuals to more than 400 individuals at both 5 and 10 radius (Figure 4).

The negative values of clustering tendency at 5m show a species trend to regularity, although at 10m the third quartile of neutral species show positive values, meaning clustering tendency, however this difference was not significant. We found no differences in the local dominance between accumulator and neutral species; however the accumulator species show lesser dominance that neutral species (Figure 4).

The ISAR at 5 and 10 m was highly correlated with the average Inverse Simpson Index calculated at these scales. There was significant difference between accumulator and neutral species at 10m, the accumulator species show higher values of Inverse Simpson Index that neutral species (Figure 4).

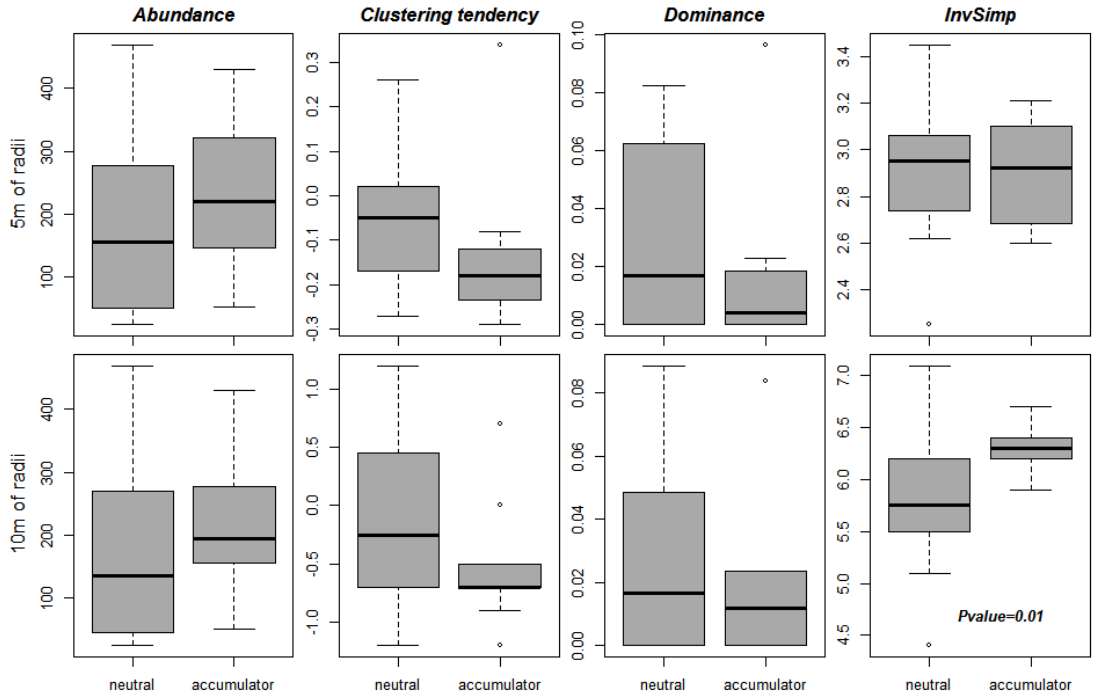

Figure 4. Relationships between neutral and accumulator species at the 5 and 10 m scales. Abundance: with the total abundance in the plot (i.e. number of individuals) of each species. InvSimp: Inverse Simpson index; Pvalue, significance with Kruskal-Wallis test. Note that at this scales no species behaved as repeller.

Discussion

The results obtained in this study, unlike previous studies in Barro Colorado Island (BCI) and Sinharaja, show that a significant number of species act as accumulators of

diversity. In fact, more than 50 % of species behave as accumulators at 5m scale and a high number maintain this behavior up to 20 meters. Several authors (Maestre and Cortina 2005, Wiegand et al. 2007a, Brooker et al. 2008) suggest that in the harshest environments species tend to improve their surrounding environment, which results in a strong spatial structuring of the community.

Our results show a high spatial dependence, contrary to what could be expected from Neutral Theory (Hubbell 1979, Hubbell et al. 1999, 2001). About 50% of the species of this ecosystem tend to be diversity accumulators, even after removing the spatial heterogeneity, that could be a cause of the aggregation of species because of habitat association (Diggle 2003, Wiegand and A. Moloney 2004). The different responses observed in this study with relation to the work of Wiegand et al. (2007a) were to be expected, since in the dry forest, the species suffers a water limitation that restricts the acquisition of resources. Under these conditions the importance of negative interactions is reduced and increases the importance of positive relationships (Callaway 2007), so it is expected that positive interactions such as facilitation would be more important and consequently accumulator species would predominate over repeller ones.

As Wiegand et al. (2007a) note, the ratio between conspecific and heterospecific stems might be influencing the responses of accumulation of species, due to the fact that species with highly clustered distributions would have a greater number of conspecific stems and fewer heterospecific and this effect will reduce the ISAR because fewer heterospecific stem in a neighborhood would also comprise fewer species (Wiegand et al 2007a). In our study the values of the ratio conspecifics-heterospecific are several times lower than those observed in BCI and Sinharaja. The main difference occurs in the number of conspecific stems; in our study, at 10 meter radius, the maximum number of conspecific stems is 1.4 compared to 4.71 in BCI and 7.71 in Sinharaja. On the contrary, the average number of heterospecific individualsis comparably high 22 stems in REMA compared with 15.8 in the BCI and 24 Sinhajara. In BCI and Sinhajara the clustering tendency of the main species attain Δ_{tt} values of 4.3 and 7.4 respectively, while in the REMA the maximum value is 1.2 at 10m. The value of the average local dominance in REMA (0.99) is inferior to those found in BCI and Sinhajara (0.26 and 0.24 respectively). The Janzen - Connell hypothesis proposes the negative density

dependence as an explanation for the high diversity in the tropics (Janzen 1970, Connell 1971), our results show a segregation of conspecific individuals, this reduction of the dominance of species increases diversity (Bazzaz 1975, Huston 1979, Armesto and Pickett 1985, Crawley 1997).

According to the Janzen - Connell hypothesis, juveniles would have a more clustered distribution that adult individual, so we expect that juveniles were highly clustered and show segregation between species, reducing the proportion of accumulator species. On the other way, adults individuals show intraspecific segregation (Bagchi et al. 2011), increasing the proportion of accumulator species. Contrary to our expectations, among the juveniles, a large proportion of species acted as accumulators and this effect was more important in short ranges, less than 10 m of radius. When considering only adult individuals, accumulator species were also important, but the proportion was higher at scales between 10 and 20 m of radius. The accumulator behavior among the larger individuals is more frequent when considering the diversity of larger individuals than when considering small individuals. This could signify that juvenile individuals are independent of adult individuals.

Contrary to the neutral hypothesis proposed by Hubbell the results show that in these ecosystems, that support a high climate stress, the positive plant-plant relationships play an important role for maintaining diversity. The species that act as accumulators has shown to be a significant richness fraction of this forest. The species in tropical dry forest show a low degree of clustering with its conspecifics as proposed by Janzen - Connell. This low degree of clustering contributes to the accumulator behavior of species. Interestingly, the behavior of the species changes depending on their size and we have observed that the large and small individuals operate independently of each other.

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CAPÍTULO 4: DIVERSITY STABILITY AT THE WHOLE COMMUNITY SCALE DEPENDS ON PLANT-PLANT INTERACTIONS SHIFTS ALONG CO-OCCURRING STRESSORS IN TROPICAL DRY SCRUBS

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Abstract

Background: Biotic interactions and shifts between them have strong effects on plant diversity. Facilitation would expand species distribution across environmental gradients and increase the extent of suitable habitats into physically harsh environments thus affecting diversity at several community scales, the bare-canopy dichotomy or the whole community. How nurses modulate diversity when several stressors co-occur and at what community scale these effects are produced remains poorly explored. Our working plan allows evaluating the effect of nurses on the biodiversity and the changes produced by biotic and climatic stressors. In addition, well known facilitation effects at the pair-wise species level are not necessarily translated to some higher level community properties because compensatory processes could yield more stable diversity outputs and dynamics.

Methodology/Principal Findings: We selected localities with contrasted grazing pressure and at four altitudes. In each plot, 20 mature *Croton* individuals and correspondent surface in open areas were selected and recorded all perennial plants. Fitted non linear models revealed a negative effect of the open microsites on richness and cover, these effects were influenced by the grazing and the altitude. The biotic

interaction effects measured with different indices were affected by the altitude and grazing. The effects were significant at microhabitat but, were not translated at plot scale.

Conclusions/Significance: Our results support our expectations since the magnitude of the effects of ecosystem engineers/nurse in species diversity and productivity vary along environmental gradients and at contrasting spatial community scales. Thus in zones with higher environmental stress and higher grazing pressure, the engineering plants effect is higher. Diversity stability at the whole community scale seems to be the norm with null effects of stressors on some community properties in spite of the existence of net effects when they are surveyed at smaller community scales such as the pair-wise differences between nurse and open areas.

Introduction

To unveil mechanisms driving species composition and maintenance of species diversity in plant communities has remained central to ecology during the last decades (Callaway 2007). The complexity of plant-plant interactions and specially positive ones have strong species specific effects on plant diversity by means of directs or indirect effects (Bertness and Callaway 1994, Callaway 1997, Crain and Bertness 2006). The common and extended occurrence of positive interactions points out that plant species may not always be distributed independently of each other (Choler et al. 2001). Positive interactions would expand species distribution across environmental gradients and increase the extent of suitable habitats –realized niche extension- into physically harsh environments where some species would not be able to survive (Crain and Bertness 2006). In consequence, the presence of a ´nurse´ species able to modify the environment by reducing the frequency and intensity of some physical constraints, disturbance or stress, leads to ameliorate habitat conditions for less tolerant species and locally increase species diversity (Hacker and Gaines 1997).

Bertness and Callaway (Bertness and Callaway 1994) proposed a simple but smart model to describe the relative frequency of competition and facilitation along gradients of physical stress or ecosystem productivity. The basic idea of the so-called stress

gradient hypothesis -SGH- is that facilitation may be especially common where harsh conditions would restrict plant's resource acquisition, and amelioration of them would favor growth to the extent that the benefits accrued outweigh the negative, competitive impact of growing in close association (Maestre et al. 2005, Cavieres and Badano 2009). In their seminal paper, Bertness and Callaway (Bertness and Callaway 1994) explicitly suggested this type of interaction should be especially critical "under high physical stress and in communities with high consumer pressure". Although the ´stress´ term is extremely controversial (Korner 2003) because it depends on the organisms and the range of environments considered (Crain and Bertness 2006), it can be easily related to productivity gradients and so, easily integrated in current modifications of the hypothesis (Maestre et al. 2009). A huge effort has been devoted to describe the existence of facilitation in very different ecosystems(Maestre et al. 2009) and to explain the mechanisms involved (Bertness and Callaway 1994, Maestre et al. 2005). However how it can affect diversity at the whole community remains almost unsolved (Cavieres and Badano 2009). Even more and in spite of the common occurrence of the two most recognized types of limiting forces, herbivory and climate stress, to our knowledge there is almost no information of the outcome of plant to plant interactions at the whole community level when these two gradients overlap (but see (Soliveres et al. 2011) for a pair-wise species interaction model). To know how both stressors may modulate the outcome of facilitation at the whole community seems critical to understand mechanisms affecting diversity in those ecosystems where these stressors are major drivers influencing plant community dynamics and composition such as in drylands (Whitford 2002).

In arid and semi-arid conditions plant performance is limited by water availability and nurse plants are critical modulate community diversity and ecosystem functioning by means of the shading and trapping effect of nurse plants (Escudero et al. 2004). As a consequence plant cover frequently occurs as conspicuous patches embedded in a bare ground matrix (Aguiar and Sala 1999). These ecosystem hubs may affect each species plant performance but also the diversity of the whole community by attenuating harsh conditions (Maestre and Cortina 2005) and also by serving as protectors from predation (Aguiar and Sala 1999). It is also well known that plant interactions commonly comprise positive and negative effects operating simultaneously (Callaway 1997) and

that local community attributes outcome may be profoundly affected by the type and composition, the shape, and size of nurse patches (Aguiar and Sala 1999), which in advance may also change over time and with environmental conditions (Callaway 1997, de la Cruz et al. 2008).

A huge research effort has revealed differences in species richness and other community attributes between cushions and open areas (Cavieres and Badano 2009) by using well known estimators of cushion effects based on pair-wise comparisons between these two microsites (see (Armas et al. 2008)). However, to our knowledge these studies emphasizing species dynamics have not been scaled up to the whole community level. This is critical because if we want to know how facilitation affects diversity at this community level we should evaluate their effect at this scale and not simply at the microhabitat level (Cavieres and Badano 2009). Important research efforts have highlighted that species diversity-stability relationships are the norm at the whole community level due to compensatory species dynamics (TILMAN and DOWNING 1994, Ives et al. 1999) although recent models suggest diversity stability may be multifaced and context dependent (Houlahan et al. 2007). Thus we have modeled some community attributes such as richness at two spatial scales (microhabitat and community) by combining explicit comparisons between canopied and bare zones with the specific evaluation of these two scenarios at both scales.

With this in mind we have explored the outcome of the nurse effects in a system model located in the Ecuadorian region. Although some works have explored the relevance of facilitation on stressful systems such as the Arctic (Carlsson and Callaghan 1991), alpine (Cavieres et al. 2006), desert (Bowers 2005) and Mediterranean ecosystems (Escudero et al. 2004, Maestre and Cortina 2005) mainly by focusing on pair-wise interactions and the effect of the nurses at the cushion level, to our knowledge there are not works exploring this topic in tropical dry ecosystems, where extrapolation from other ecosystems should be done with caution. These tropical dry ecosystems have received little attention compared with other tropical ecosystems (Sanchez-Azofeifa et al. 2005). This is especially demanding since they are under severe anthropogenic pressure worldwide and their current conservation status is really critical in most regions (Janzen 1988). In Ecuador, they comprise the south western fringe of the

country and are a part of the dry ecosystems of the Tumbesian region (Espinosa et al. 2011). This is one of the regions of the world with higher endemicity in a narrow extension (Best and Kessler 1995) but also, unfortunately, one of the most threatened and less known (Janzen 1988). The *dry montane scrub* system is especially suitable for our work because the community is dominated by a unique nurse/engineer along a very long altitudinal gradient that is subject to different grazing pressures.

We evaluated the role of the local nurse/engineer, *Croton wagneri* on several community attributes and their response to climatic and biotic stress. We used the altitude as surrogate of climatic stress (see (Körner and Paulsen 2004) for the use of altitude as a surrogate of climate) and localities subjected to different cattle grazing pressures as surrogate of biotic stress Our working hypothesis is based on two complementary ideas: i) nurses increase the diversity in this ecosystem because many species recruit successfully only beneath their canopies but the importance of this facilitation decreases in areas with lower abiotic stress (with respect to water availability and temperature), ii) this primary effect is modulated by herbivory pressure - i.e., biotic stress - which can force some plants to survive only under nurse canopies even under relatively milder climate conditions. This implies the role of nurses as modulators of diversity at the whole community may outcompete the effect of climate stressors if grazing co-occur.

Materials and Methods

Ethic statement

We were granted permission to field-work on site from the land-owners. Field studies did not involve endangered or protected species.

Study Site and Natural History

Our study was conducted in the Ecuadorian *mountain dry scrub* ecosystem which occurs in some interandine dry valleys between 1400 and 2500 m (Figure 1). Vegetation is dominated by *Croton wagneri* (Müll) Arg. an endemic shrub but locally abundant

*(*Ulloa and Jorgensen 1995) up to 2 m high that forms conspicuous patches interspersed in open areas along a 900 m altitudinal gradient. It grows together with other rare xerophytic and spiny perennial species such as some columnar cacti and *Euphorbia* species and some scattered trees up to 7 m high such as *Acacia macracantha* Humb. & Bonpl. *ex* Willd. and *Bursera graveolens* (Kunth) Triana & Planch (Sierra 1999). This vegetation type is a shrubby variant of the Tumbesian dry forests that extends from north Peru (Harlling 1979) to south Ecuador (Espinosa et al. 2011). This vegetation covers a very rough territory of very difficult access which is dissected by some rivers conforming impressive narrow canyons.

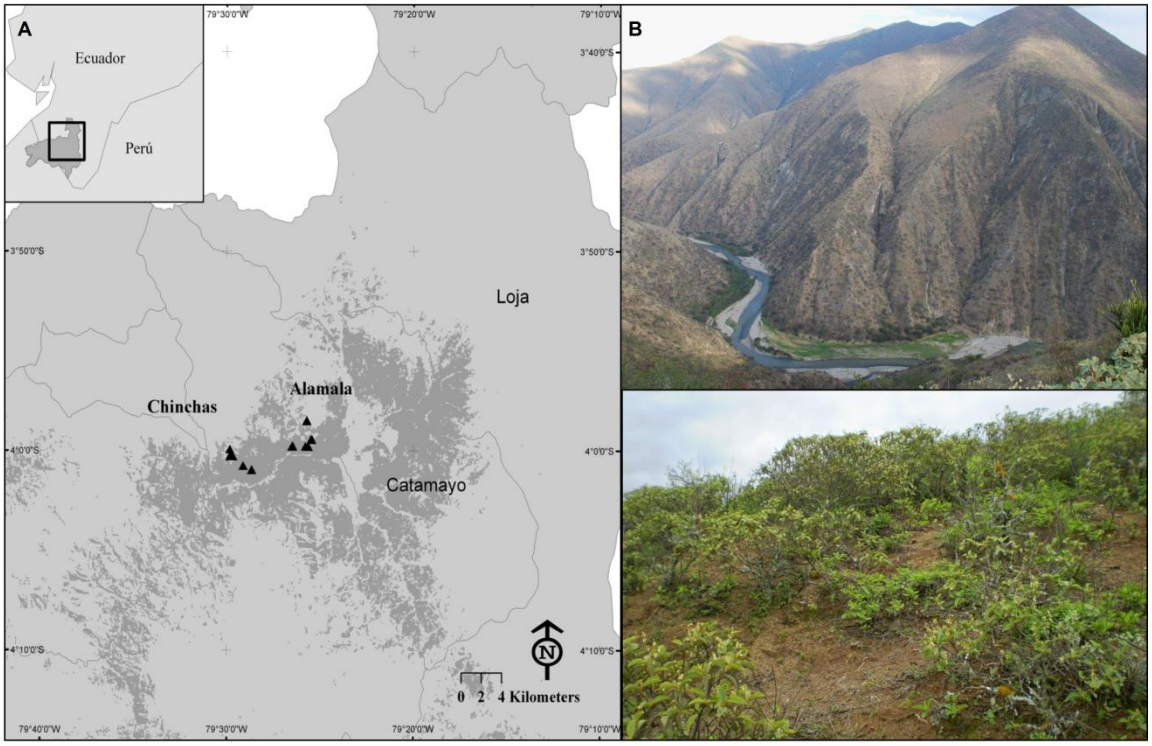

Figure 1. **Location of the research area**. A/ Ecuadorian *dry montane scrub* ecosystem (dark grey) and the surveyed communities which are located in two localities Alamala (4º0' 16.37"S; 79º29' 51.07"W) and Chinchas (3º59' 51.07"S; 79º26' 30.93"W). Coordinates correspond to the centroid of each locality. B/ View of the Catamayo river canyon in the upper half and of *Croton wagnerii* patches during the rainy season in Alamala.

We selected two close localities, named Chinchas and Alamala, located 20 km apart in the valley of Catamayo (Loja province, Ecuador) whose vegetation is dominated by our

engineer/nurse plant *Croton wagneri.* They constitute an ideal natural system model because they share the same climate, slope, orientation, altitude range, and, obviously, vegetation, differing only in the intensity of grazing by cattle. Chinchas (with an altitude range from 1490 m to 2090 m) is managed with cattle grazing whereas Alamala (from 1530 m to 1950 m) remains undisturbed. Grazing in Chinchas is temporary during the short rainy season (between January and May) with stock densities of 1 to 3 animals/ha. Average mean temperatures in the close Catamayo airport (1500 m) are 27.5°C, with average maximum monthly temperatures of 30.8°C and minimum of 17.9°C. Average annual precipitation and evapotranspiration in this station are 383 mm and 1112 mm, respectively (Richter and Moreira-Muñoz 2005). From May to December rainfall does not compensate the local evapotranspiration causing an intense water shortage.

Vegetation Sampling

At each locality, the altitudinal range occupied by *Croton* was evenly divided to locate four sites. We established two 30 x 30 m plots in each altitudinal site, separated by no more than 500 m in horizontal distance (mean distance was 200 m). Each plot was located haphazardly on a representative and homogenous portion of the scrubland, avoiding ravines, cliffs, and whatever object/structure that could bias our estimates of taxonomic diversity. To estimate plant cover per plot we located four 30 m-long transects perpendicular to the direction of the maximum slope and separated by a distance of 8 m. In each transect we placed 20 contiguous 1.5 x 1.5 m quadrates and recorded the presence and percentage cover of each perennial plant species. Total cover in each plot, which is known as a good surrogate of primary productivity in semi-arid environments (Maestre and Escudero 2009) was estimated from the average perennial plant cover across the 80 quadrates taken in a plot.

We also characterized the patchy structure of the vegetation by means of the line-intercept method (Tongway and Hindley 2004) on each transect. We measured the size of each patch (perennial plants aggregations in which *C. wagnerii* was always present) and interpatch (bare soil) cut by transects. When a patch was intercepted by the transect we measured both its length and width (this one as the maximum perpendicular measurement). For each plot, we calculated several indices of patch structure from this

data, such as patch number, average patch area (PAI), average interpatch length (AIL), maximum interparch length (MAXIL) and minimum interparch length (MINIL) (Tongway and Hindley 2004).

Patch and interpatch features

In each plot, 20 mature *Croton* individuals were randomly selected and tagged. We measured the maximum and perpendicular minimum axes of each nurse plant/patch to estimate its canopy area by approximating it to that of an ovoid (Cavieres and Badano 2009). We recorded all perennial plant species found, abundance and their percentage cover. In addition, the total area under their canopies was also sampled with 0.5 x 0.5 m grid quadrates to facilitate the translation of the corresponding canopy surface to open areas. In an adjacent and haphazardly chosen open area (at least 1 meter away from any *Croton* individual), each tagged *Croton* area and shape was replicated, i.e., we delimited polygons with exactly the same area (the same number of 0.5 x 0.5 m quadrates). Richness and cover of all perennial plant species was recorded in the same way than under shrubs. On the basis of species abundance we computed the inverse Simpson index in each open and nurse/patch areas. In addition the species abundance within all 20 patches and corresponding nurse areas in each plot was combined to compute plot estimates of Inverse Simpson index in patch and open areas respectively.

Indices for biotic interaction effects on plant diversity and on habitat expansion

We used eight complementary indices (table 1) for evaluating the importance, intensity and direction of the effects of *Croton* over plant diversity at two scales: the nurse-open dichotomy and the whole community. These indices are based on the simple idea that a higher number of individuals and/or a greater cover of a given species in some of these microsites should be indicating a superior environmental conditions experienced in this microsite/plot for this species (Choler et al. 2001, Armas et al. 2004). These indices allow us to establish the net balance of the interaction between *Croton* and different plant species along the environmental abiotic and biotic stress gradients.

Three indices were proposed for estimating the habitat expansion of each individual species, the AOF, RIIos and IIS (Table 1). Considering those species that at the plot level only occurred under *Croton* conditions but never in open areas.

Table 1. **Description of the interaction indices for richness and cover.**

Indices	Calculation	Application/scale	Description
Relative Interaction Index with plant cover (RIIc; Armas *et al*. 2004)	$\frac{C_{nurse} - C_{open}}{C_{nurse} + C_{open}}$	Microhabitat / plot	It is calculated as the difference in cover between the nurse and open microsites, relative to the sum of cover in the two microsites. This index ranges from –1 to 1, with positive values indicating facilitation and negative values competition.
Relative Interaction Index with plant richness (RIIr)	$\frac{R_{nurse} - R_{open}}{R_{nurs\sim} + R_{open}}$	Microhabitat / plot	It is calculated as the difference in richness in nurse and open microsites, relative to the sum of richness in the two microsites. This index ranges from –1 to 1, with positive values indicating facilitation and negative values competition.
Absolute importance of the Interaction with plant cover (AIIc)	$C_{nurse} - C_{open}$	Microhabitat / plot	It measures the difference in cover of perennial plants between the nurse and open microsites in absolute terms. Positive values indicate facilitation and negative values indicate competition.
Absolute importance of the Interaction with plant richness) (AIIr)	$R_{nurse} - R_{open}$	Microhabitat / plot	It measures the difference in richness of perennial plants between the nurse and open microsites in absolute terms. Positive values indicate facilitation and negative values indicate competition.
Importance of the biotic interaction for the most abundant species (IIAS)	$\frac{\sum(C_{nurse/specie} - C_{open/specie})}{\sum A_{nurse}}$	Plot	This index estimates the variation in performance between both microsites for individual species. It measures the differences of cover between the nurse ($C_{nurse/specie}$) and open ($C_{open/specie}$) micrositess for the dominant species that are scaled up to the plot level. Positive values indicate facilitation and negative values indicate competition
Absolute Obligate Facilitation Index (AOF)	$\frac{S_{nurse}}{Total\ richness}$	Plot	This index was calculated only at the plot scale. It compares the number of species that occur only under nurses with the total of species in the plot.
RII index for the number of obligate species (RIIos)	$\frac{(S_{nurse} - S_{open})}{(S_{nurse} + S_{open})}$	Plot	This index is calculated at plot level. This a relative index that compares the number of species occurring only under patches in relation to those species that occur only in open areas.
Importance index for species increasing their presence by using patches (IIS)	$\frac{(S_{nurse} - S_{open})}{Total\ richness}$	Plot	It measure the percentage of species increasing their range extend by means of the nurse

Nurse and *Open* denote respectively the microsite: under the canopy of a nurse (*Croton* microsites) and in open (bare soil, i.e., inter-patch microsites). The letter "P" indicates species that are found only in one of the two microsite at the plot level (*specialist species*). S_{nurse} and S_{open} correspond to the species cover under the canopy of a nurse (*Croton* microsite) and in open (inter-patch microsite), respectively. A_{nurse} and A_{open} correspond to the sampling area in a nurse and in open micrsites. Finally, *Total richness* is the total number of species in the plot.

Data Analysis

Model fitting

Our statistical models were made at two levels; microhabitat and plot. In each level, we analyzed; i) the community attributes on each microsite (not paired data) and ii) biotic interactions exploring at each level the variation between patch and bare areas (paired data). The community attributes were evaluated for each microsite (nurse and open areas), while the biotic interactions were evaluated with indices of interaction

All community responses were modeled as a function of altitude as the surrogate of climate stress, grazing and their interaction and also included plant cover as a covariate to control for the primary productivity effect on diversity. Microsite was also included as an additional covariate in the case of not paired data. In the microhabitat-level models we evaluated also the convenience of including quadratic terms of altitude and of the altitude-grazing interaction to account for non-monotonic responses along the gradient. In addition we included some other covariates such as minimum interpatch length (MINIL) as a surrogate of patch structure and the patch size.

We included plot identity as a random factor (i.e., we fitted mixed models with all other predictors as fixed factors) to account for spatial autocorrelation and other potential bias due to some unobserved trends related to our field experimental design (Warren 2010).

As most of the responses that we recorded were asymptotically bounded between a minimum and a maximum value, we used non-linear regression (Ritz and Streibig 2008) to fit models based in 2-parameter logistic functions (i.e., $= \frac{e^{a+bx}}{1+e^{a+bx}}$), expanded an

translated to fit the responses between the corresponding bounding limits (Legendre and Legendre 1998). Assuming a logistic response is mostly analogous to the usual approach in ecology of fitting binomial GLM's to proportions or to responses bounded between 0 and 1 (Crawley 2007) but additionaly, this releases the analysis from the necessity of transforming the data to fit any of the usual probability distributions assumed by GLM's (O'Hara and Kotze 2010, Warto and Hui 2011). We performed the usual model diagnostics and when apparent violations were found, we refitted the standard errors of the coefficients by adjusting the estimated variance-covariance matrix by means of sandwich estimators (White 1996). Statistical analysis was performed with packages stats (R Development Core Team 2011), nlme (Pinheiro et al. 2009) and nls (Bates and Chambers 1992).

Results

We sampled a total of 640 microsite (320 nurse patches and their corresponding paired open-ground areas). Average patch area was 6.26 m^2 ±6.06 sd. We recorded 26 perennial species, with an average richness per nurse of 3.4 ± 1.3 and in the open 2.3 ±1.1, the average percentage cover of plant species (excluding Croton) per nurse was 21.9% ±18.8 and 4.5 ±8.2 in each open area. The most abundant species taken all plots and individuals together are *Lantana canescens* Kunth *with 36.48%, Gaya calyptrata* (Cav.) Kunth ex K. Schum with 18.93% and *Stachystarpheta steyermarkii* Moldenke with 16.19%. Three species occurred exclusively under the *Croton* canopy whereas no species grew exclusively in open areas.

Grazing and climate effect on plant community attributes

Fitted models revealed a significant negative effect of the open microsite on richness and total cover at both microhabitat and plot scales. This effect was observed also on the inverse Simpson index but only at the plot scale (table 2). Variation in altitude induced significant negative effects in cover at both scales but did not affect species richness. At the microhabitat scale, this effect was better explained by the inclusion of a quadratic term in the model. This means that conditions on the altitude edges exerted relatively

similar effects on the target variable being different from those in the middle range (figure 2).

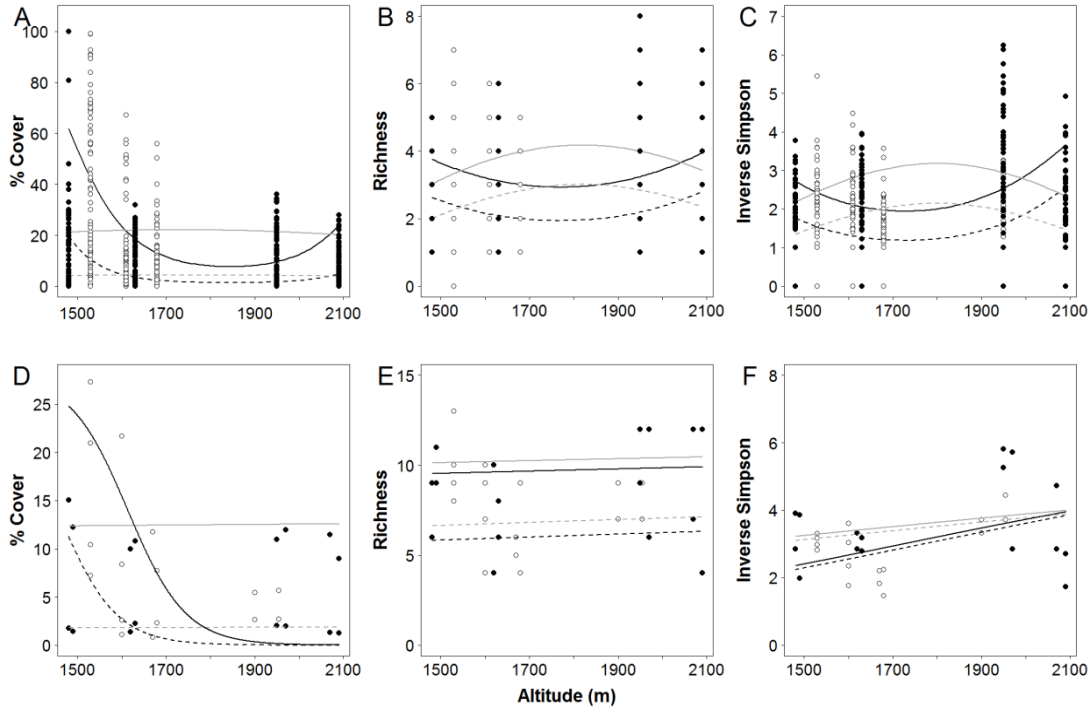

Figure 2. Fitted models to cover and diversity data. The sampled patches are marked as circles, the black circles in grazing locality and the white circles the undisturbed locality. Fitted models for each locality shown as solid line for nurse microsite and dotted line for open microsite, black lines for undisturbed locality and darkgray for grazing locality.A, B and C models at microhabitat scale, D, E and F models at plot scale level.

Grazing showed a significant and negative effect on cover, richness and inverse Simpson at the microhabitat scale and over cover at the plot scale. There was also a significant effect of the interaction between grazing and altitude on cover at two levels whereas on richness and inverse Simpson was significant only at microhabitat level. This means that the effects of altitude are different in grazed *vs* ungrazed plots except in the case of richness and inverse Simpson at the plot level where this interaction was no significant (table 2).

Table 2: Estimates of fitted models for community attributes

	Microhabitat			Plot		
Predictor	**Cover**	**Richness**	**Inverse Simpson**	**Cover**	**Richness**	**Inverse Simpson**
Intercept	***70.91740***	n.s	n.s	***23.73256***	n.s	n.s
Altitude	***-0.08061***	n.s	n.s	***-0.01534***	n.s	n.s
Altitude^2	***0.00002***	n.s	n.s	n.i	n.i	n.i
Grazing	***-75.70390***	**-32.17899**	***-42.87804***	***-25.06251***	n.s	n.s
Altitude:Grazing	***0.08365***	**0.03658**	***0.04961***	***0.01539***	n.s	n.s
Altitude:Grazing2	***-0.00002***	**-0.00001**	***-0.00001***	n.i	n.i	n.i
Microsite/open	***-1.80818***	***-0.59133***	***-0.63202***	***-2.43938***	***-1.21048***	n.s
MINIL	n.s	n.s	n.s	n.i	n.i	n.i
Productivity	***0.01926***	n.s	n.s	n.s	n.s	n.s

MINIL: minimum interpatch length, Microsite/open: open habitat, and Productivity: surrogate of primary productivity, measure with the total ground cover in the plot. Significance is show in bold ($p < 0.05$), and bold-italics ($p < 0.01$). n.i: Variables not included in the model. n.s: Variables not significant

Grazing and climate effects on biotic interactions indices

Variation in altitude induced negative and significant effects in AIIc, RIIr and AIIr at microhabitat scale but only in the case of the cover-based AIIc index at plot scale. The effect of altitude on RIIc at the microhabitat scale was better explained by the inclusion of a quadratic term in the model. There was a significant interaction between grazing and altitude in these significant models which suggests that effects of altitude are different in grazed *vs* ungrazed zones at the microhabitat scale. The AIIc was the unique index that was significantly affected by this interaction at the plot scale (Table 3, see also figure 3).

Table 3: Estimates of fitted models for our interaction indices.

	Microhabitat				Plot			
Predictor	**RIIc**	**AIIc**	**RIIr**	**AIIr**	**RIIc**	**AIIc**	**RIIr**	**AIIr**
Intercept	***-47.8687***	***4.2190***	***3.9845***	n.s	n.s	**46.8679**	n.s	n.s
Altitude	***0.0590***	***-0.0034***	***-0.0018***	**-0.0008**	n.s	***-0.0329***	n.s	n.s
Altitude2	***-0.0002***	n.i	n.i	n.i	n.i	n.i	n.i	n.i
Grazing	***68.5615***	***-5.5396***	***-5.6090***	***-3.1951***	n.s	***-58.1635***	n.s	n.s
Altitude:Grazing	***-0.0804***	***0.0033***	***0.0033***	***0.0020***	n.s	***0.0360***	n.s	n.s

Altitude:Grazing2	***0.00002***	n.i	n.i	n.i	n.i	n.i	n.i	n.i
MINIL	***-2.4416***	**-1.0757**	n.s	**-1.0069**	n.i	n.i	n.i	n.i
Patch Size	n.s	**-0.0196**	***-0.0363***	n.s	n.i	n.i	n.i	n.i
Productivity	n.s	**0.0124**	n.s	n.s	n.s	n.s	n.s	n.s

MINIL: minimum interpatch length, PatchSize: size of sampled patch, and productivity which is a surrogate of primary productivity estimated by means of the total plant cover in the plot. Significance is show in bold ($p < 0.05$) and the bold italics ($p < 0.01$). n.i; Variables not included in the model. n.s: Variables not significant

The indices AIIr, RIIc and AIIc were affected by our surrogate of patch structure at the microhabitat level, the so-called MINIL (minimum interpatch length). Patch size affected negatively the AIIc and RIIr indices at microhabitat scale.

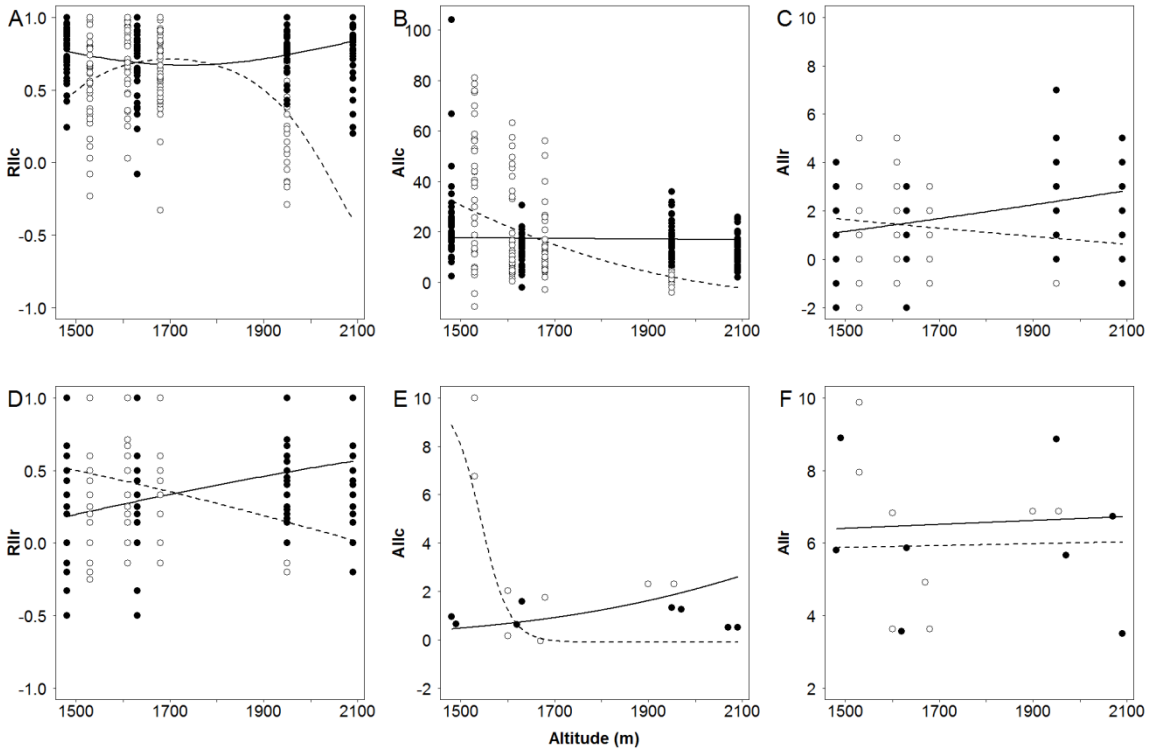

Figure 3. Fitted models to the interaction indices. RIIr; Relative Interaction richness Index, RIIc; Relative Interaction cover Index, AIIr; Absolute Importance richness Index, AIIc; Absolute Importance cover Index. The sampled patches are marked as circles, the black circles in grazing locality and the white circles the undisturbed locality. Fitted models for each locality shown as solid line for grazing locality and dotted line for undisturbed locality. A, B, C and D models at microhabitat level, E and F models at plot level.

Species specific effects of grazing and climate

Altitude and grazing had not significant effects on the AOF, RIIos and IIS biotic indices computed at the plot scale (table 4).

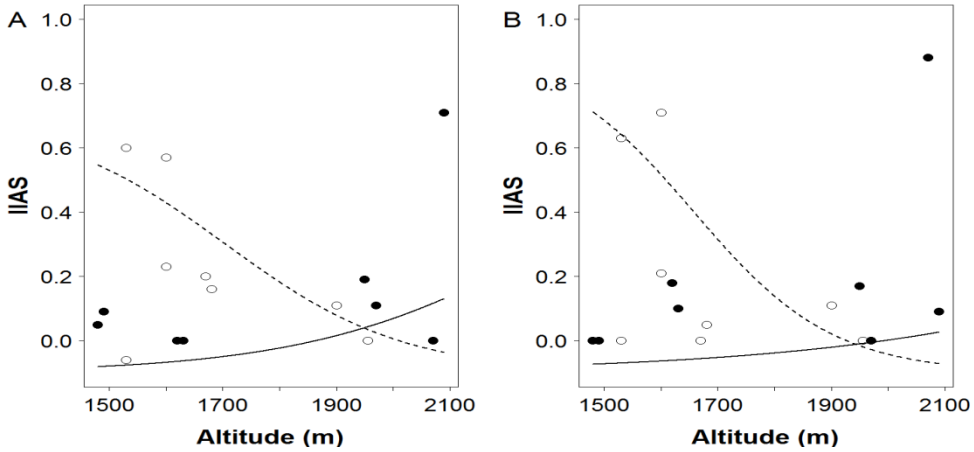

Figure 4. Fitted models to individual species performance indices. IIAS; Importance of biotic interaction for the most abundant species with *Croton wagnerii* (A), *Opuntia quitensis* (B). The sampled patches are marked as circles, the black circles in grazing locality and the white circles the undisturbed locality. Fitted models for each locality shown as solid line for grazing locality and dotted line for undisturbed locality.

On the other hand the performance of the most abundant species measured with the IIAS index is affected by grazing and the interaction between grazing and altitude at least in the case *Croton wagnerii* (saplings living under the canopy) and *Opuntia quitensis*. These two species showed an increase in the index (i.e., the difference between cover inside the patch and open areas increased) in the highest elevations under grazed conditions. The effect of grazing was also significant, showing a reduction in the values taken by the index in the grazing zone. In addition, our productivity surrogate affected positively the IIAS of *Stachystarpheta steyermarkii* and negatively the IASS of *Opuntia quitensis* (Table 4, see also figure 4).

Table 4: Estimates of fitted models for our individual species performance indices.

	Plot			Especies/IIAS							
Predictor	**AOF**	**RIIos**	**ISS**	**Croton**	**Gaya**	**Mimosa**	**Opuntia**	**Steyen**	**Lantana**	**Baccharis**	**Onoseris**
Intercept	n.s	n.s	n.s	n.s	n.s	n.s	**14.1379**	n.s	n.s	n.s	n.s
Altitude	n.s	n.s	n.s	n.s	n.s	n.s	**-0.0059**	n.s	n.s	n.s	n.s
Grazing	n.s	n.s	n.s	**-19.8219**	n.s	n.s	**-15.1266**	n.s	n.s	n.s	n.s
Altitude:Grazing	n.s	n.s	n.s	**0.0102**	n.s	n.s	**0.0078**	n.s	n.s	n.s	n.s
Productivity	n.s	n.s	n.s	n.s	n.s	n.s	**-0.0854**	**0.0456**	n.s	n.s	n.s

Significance is show in bold ($p < 0.05$) and the bold-italics ($p < 0.01$). Croton: *Croton wagnerii*, Gaya: *Gaya calyptrata* , Onoseris: *Onoseris sp*., Opuntia: *Opuntia quitensis* , Steye: *Stachystarpheta steyermarkii*, Lantana: *Lantana canescens*, Bacharis: *Baccharis salicifolia*. Productivity: is a surrogate of primary productivity estimated by means of the total cover in the plot. n.s: Variables not significant

Discussion

The most limiting forces to plant performance, herbivory and climatic harshness, are well known filters of the composition and structure of plant communities determining which plants from the regional pool can coexist under specific conditions (Jones et al. 1997, Callaway 1997, Graff et al. 2007). The co-occurrence of both stressors exerted a synergistic effect on plant community attributes and species performance (Graff and Aguiar 2011). We also know that positive interactions can expand species ranges far away from physiological limiting gradients (Crain and Bertness 2006). Thus the presence of nurse facilitators usually has profound consequences on species performance and presence under herbivory and adverse climate conditions, enlarging their niche and probably inducing a local increase in species diversity (Hacker and Gaines 1997). Surprisingly, current knowledge of how the co-occurrence of these stressors may affect diversity and how this combined effect is altered through the mediation of nurses is really poor (see (Soliveres et al. 2011)). This is especially necessary since the effect of individual stressors at the species level seems to be markedly significant, but we do not know if these specific effects are scaled up to affect whole community level attributes and if the co-occurrence produces additive or

synergetic effects. Our results seem to confirm our idea that the primary effect of nurse amelioration to stressful climate conditions is modulated in a second stage by grazers. Thus grazing pressure would be forcing some plants to occur only under the protective canopy of nurses even under relatively mild climate conditions where the facilitated species could occur without this help if grazers were absent. This implies that the expected response of facilitation along stress gradients can hardly be found and helps to explain most discrepancies found in relation to the SGH universality (Maestre et al. 2009). As expected our results showed the concurrence effect of both co-occurring stressors was really impacting.

Nurse effects on diversity can be also interpreted under the framework of physical ecosystem engineering which is the process by which some species, the ecosystem engineers, change the distribution of materials and energy in natural landscapes via non-trophic interactions with their abiotic environment (Jones et al. 1997). The magnitude of the effect of these ecosystem engineers change across the stress gradient (Crain and Bertness 2006). The results of our study support our idea that *Croton* is an ecosystem engineer and the magnitude of its effects profoundly affect some community attributes such as species diversity and cover along environmental gradients. Moreover, our results show that the over-imposed biotic stress (grazing pressure) alters the importance of positive–negative interactions on the former climate gradient (Graff et al. 2007). Thus under the pressure of herbivores the importance of the engineering nurse plants is extended even to zones with relatively benign climates.

Community attributes along co-occurring stress gradients

Pioneering studies have suggested that among local-scale processes sorting community composition, competition regulates richness under high levels of productivity, while limited physiological tolerances to abiotic stress or to disturbance reduce species recruitment, and thus richness, at low levels of productivity (Grime 1973). Our results showed some discrepancies and suggested that only the microsite differences at both spatial community scales together with the effect of grazing at the microhabitat scale affected plant diversity being higher under canopies and in not grazed areas. However it is worth to note that there is also a significant interaction between altitude and grazing

at the latest scale. Thus richness and inverse Simpson under grazing pressure seems to mimic a humped pattern along elevation with a maximum at intermediate elevations being restricted at both edges of the altitudinal range, in concordance with Grime (Grime 1973), whereas under not disturbed conditions, this shape is inverted suggesting the existence of higher diversity levels on both edges of the climate gradient. Although this U-shaped relationship seems counterintuitive, Mittelbach et al. (Mittelbach et al. 2001) found a substantial number of such a type of shapes after reviewing the relationships between productivity and richness. Scheiner and Jones (Scheiner and Jones 2002) suggested that the U-shaped relationships may be caused for the existence of transition zones in the limits of the gradient. In our case, it would be possible that in the highest zones the increase in water availability causes a change in plant community whereas in the lowest zones, facilitation increases the richness and inverse Simpson index.

The cover response to elevation when grazing pressure is absent seems to follow a pattern concordant with the predictions of the SGH. However this pattern is significantly modified under grazing because at the highest altitudes competition may be reduced under such mild conditions simply because grazing could reduce the intensity of competition.

Plant-plant interactions along co-occurring stress gradients

In order to detect first, the existence of plant-plant interactions and second, to quantify the intensity and direction of them and their effect on diversity at the two community scales, we used a battery of indices because these parameters are not easily and univocally measured (Maestre et al. 2005). These indices were computed using both plant richness, and species cover as surrogates of community and plant performance, respectively.

Previous studies in alpine (Cavieres et al. 2006), deserts (Bowers 2005) and Mediterranean (Escudero et al. 2004) habitats have provided evidence for positive associations of plants with cushion species, being one of the most consistent findings the increase of positive associations with elevation (Cavieres et al. 2006). However,

shifts between the prevalence of positive and negative interactions trough out an elevation gradient seems to be quiet different in arid regions and Mediterranean mountains. Thus in Chilean Andes, facilitation is higher in lower zones, probably because water availability at these rear edges reaches a minimum and temperatures is higher increasing the evapotranspiration (Cavieres et al. 2006). Our results show that under the abiotic stress gradient the prevalence of facilitation seems to follow a humped pattern (see(Maestre and Cortina 2005)) with a marked shift to competition in the most benign conditions at the highest altitude where productivity is higher and a peak of facilitation at intermediate altitudes. However this finding only occurs at the microhabitat scale disappearing at the plot level, independently of using richness or cover as community attributes and not only as suggested by the RII´s but also when the Absolute Importance of the Interaction index(AII) for richness is computed. This suggests that the widely found differences at the microhabitat scale (see (Badano et al. 2010)) could shift to null if the variation in richness and cover are scaled up to the whole community. This suggest that the community is far more stable than suggested by species specific shifts between microhabitats and in accordance with the diversity-stability assumptions (TILMAN and DOWNING 1994). In addition our results also showed that this community scale is critical to understand how nurses affect diversity. Obviously the net outcome needs to be explored at the whole community and not at the usually explored microhabitat level (Cavieres and Badano 2009).

On the other hand the inclusion of grazing has a substantial impact on the pattern of biotic interactions along elevation. Facilitation tends to increase along altitude probably because the grazing pressure increase as productivity becomes higher. Such a pattern has been found in arid communities (Oesterheld and Oyarzábal 2004) where competing grass neighbors can be transformed into refuges (Graff and Aguiar 2011) changing the patterns interaction from competition to facilitation. Again this pattern is not scaled up at the whole community.

Plant performance along co-occurring stress gradients and habitat expansion

It is known that determining which one of the effects of ecosystem engineers (species diversity or performance effects) is more relevant in affecting ecosystem functions

strongly relies on identifying which species are specialists for engineered/canopied and unmodified/bare habitats and which species are habitat generalists at each study site (Badano et al. 2006). The presence at the plot level of specialist in each microsite was evaluated by means of three indices (AOF, RIIos and IIS). Neither elevation nor grazing were significant predictors which suggests that these stressors did not affect the value of nurses for expanding the habitat. This again reinforces the idea of the existence of a diversity stabilizing mechanism probably based on compensatory effects at the population/species level.

We also evaluated the response of the eight most abundant species by means of the so-called Importance of the biotic interaction index (IIAS). Only for *Croton wagnerii* and *Opuntia quitensis* we found significant effects of elevation and/or grazing. The responses were markedly different between grazed and ungrazed sites. In grazed sites the importance of facilitation is higher as altitude increase; the response in abundance at the species level was also reflected at the community level.

In conclusion the Ecuadorian *Scrub Dry Montane* ecosystem constitutes an additional example of a system in which the facilitative relationships are critical for the community at contrasting scales. In addition our results suggest that stability at the whole community scale seems to be the norm, with null effects of stressors on some community attributes such as richness and cover. This is surprising since we have detected the existence of net effects at smaller community scales. Taken all these results together we can suppose that compensatory dynamics are responsible of community stability along the environmental sharp gradients even when two stressors co-occur. Finally our results also are in agreement with our working hypothesis, at microhabitat level the importance of facilitation increased when climatic stressors increased, and under *Croton* canopies the diversity and cover is higher than in the bare soil and this difference is increased with the abiotic stress. This response was heavily modulated by grazing, in altitudes with milder climatic conditions, facilitation was maintained because grazing reduced competition and transformed the patches in refuges. So, biotic stress by consumers significantly alters the nature and strength of species interactions in ecological communities and can even swap the sign of species interactions.

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CAPÍTULO 5: PATCH EFFECT ON SOIL SEED BANK IS MODULATED BY CO-OCCURRING STRESSORS

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Abstract

Question: : i) Climate amelioration with altitude may increase seed bank density and richness by means of the improvement of above-ground vegetation performance and fertility; ii) this climate effect will most likely be modulated by herbivory; iii) we expect that under high abiotic and biotic stress conditions differences between transient and permanent bank will be small or null while the improvement of these conditions will mean an increase in the difference between these two banks; iv) at higher climatic and biotic stress the seed bank richness and abundance would be mainly controlled by the surrounding vegetation, this effect depend of the scale. **Location:** The field work was undertaken in the Ecuadorian Dry Mountain Scrub Ecosystem.

Methods: Our observational study was developed along the climatic stress gradient on two management conditions undisturbed and grazing. The effect of grazing, altitude and their interaction in the abundance and richness transient and permanent seed bank was evaluated with non-linear mixed models.

Results: Altitude, grazing and their interaction exerted a significant effect on species richness and seed abundance of the transient seed bank. At higher elevations and under grazing the transient seed bank dominated in terms of abundance, The interaction between altitude and grazing showed an opposite responses between grazing and undisturbed conditions. Finally, dominance between aboveground vegetation richness vs. belowground seed richness greatly varied along the altitudinal gradient and at different grazing intensities, but in a different way depending on the spatial scale.

Main conclusions: As expected our study demonstrates that climate acted as a key environmental filter in soil seed bank development and structure and also that grazing modulated the effect of climate on seed bank properties. In this tropical dry scrub, richness and abundance of seeds increased along the altitudinal gradient, most likely because ascending in altitude environmental conditions are improved.

Keywords: altitudinal stress, grazing, dry scrub, tropical ecosystem, above-ground control, transient vs. permanent seed banks

Introduction

The transition from seed to plant is a key process determining community structure and dynamics (Eriksson and Ehrlén 1992). As a consequence, knowledge on seed bank function and the interaction with standing vegetation has become a priority for plant ecologists (Chambers and MacMahon 1994). This seems especially critical in stressful habitats such as arid and semiarid ecosystems where seed banks are important ecosystem components (Busso and Bonvissuto 2009) that allow species persistence during unfavorable periods (Kinloch and Friedel 2005) and promote community stability by reducing effects of environmental stochasticity (Fenner 1995).

In stressful ecosystems, a two phase vegetation structure prevails with patches interspersed in bare ground areas. Several studies have found the profound effect of plant patches and their dynamics on seed bank properties for instance seed bank density and richness are much higher inside patches than in bare areas (Pugnaire and Lázaro 2000, Caballero et al. 2008, Busso and Bonvissuto 2009). This spatial structure is

related to higher seed production within patches (seed source effect) and to the capability of patches to trap seeds from surrounding environments (trapping effect) (Flores and Jurado 2003, Bullock 2004). Plant patches prevent seed losses due to superficial run-off and act as seed sources during secondary dispersal. Deepening into the knowledge of how this "patch effect" on seed bank properties varies with the presence and intensity of some stressors has become a research priority (*****) however, the mechanisms that modulate the "patch effect"along stress gradients when several stressors co-occur remain unknown. For instance, several evidences highlighted the important influence of grazing conditions on plant-plant interactions, patch structure and dynamics, and also on soil seed bank composition and structure (Cavieres and Arroyo 2001, Funes et al. 2003, Miller and Cummins 2003, Ma et al. 2010a) but to our knowledge there is no information on how this structuring force of soil seed banks is affected by other co-occurring stress gradients (but see Ortega et al. 1997). This is especially demanding since it is also known that taken independently climate and herbivory stressors, they profoundly affect the relationship between the seed bank and the above-ground vegetation (Hopfensperger 2007, Chaideftou et al. 2008) and even the relationships between the transient and permanent seed banks (e.g. (Milton 1939, Thompson 1978, Hopfensperger 2007).

Altitude is a good surrogate of environmental gradients because if surveyed samples are well located, most climate variables vary in a predictable fashion (see (Korner 2003). Studies on the effect of altitude on seed bank properties have shown contrasting results, some studies reported richness and density decreases with altitude (Ortega et al. 1997, Cummins and Miller 2002) and others found positive trends between altitude and seed bank properties (Funes et al. 2003). Although some mechanisms have been proposed to explain these apparent contradictory results, they remain inconclusive. Some authors explained the higher seed densities on more stressful edges due to seed longevity increase at low water soil conditions (Ortega et al. 1997; Cavieres & Arroyo 2001; Turner et al. 2006). Otherwise, wet and mild (i.e less stress) conditions usually reduce seed viability (Walck et al. 2011) because high soil moisture may favor fungal pathogens leading to reduced seed persistence in soil (Wagner and Mitschunas 2008, Walck et al. 2011). However, the better performance of species in benign sites allow the higher production of seeds (Miller & Cummins 2003; Ma et al. 2010). We hypothesize

that these differences are simply a confounding interpretation related to the contrasting behavior and weight given in each research to the permanent (viability) and transient bank (fertility) compartments. The knowledge about how the balance between both soil seed compartments shifts along environmental gradients is also critical and may help to interpret the role of seed banks on community persistence and dynamics.

Similarly to altitude, evidences of the impact of grazing on the size, richness and composition of seed banks are variable (Kinloch and Friedel 2005), some studies suggested positive responses of seed bank abundance to grazing (Navie et al. 1996), while others found neutral effects (Meissner and Facelli 1999, Kinucan and Smeins 2008) and a few studies detected negative impacts on the seed bank with increasing grazing pressure (Bertiller 1996). These apparently opposed effects of grazing have been relied on its effect on above-ground vegetation and more specifically on fertility increase which in turn could reduce seed bank replenishment (Pazos et al. 2007, Kinucan and Smeins 2008, Kassahun et al. 2009). In parallel, grazing usually affects more intensively the perennial component (Bestelmeyer et al. 2003) improving the conditions for annuals species (Navie et al. 1996) which could increase the size of their soil seed bank.

On the other hand, it is also well-known that stressful systems tend to maintain a high similarity between above and below ground species composition (Thompson and Grime 1979, Henderson et al. 1988, Hopfensperger 2007). The high similarity found between the seed bank and the vegetation composition in arid communities is based on the unpredictable growing conditions that favor species provided with persistent seed banks and lead to a high similarity to parent vegetation (Henderson et al. 1988). The similarity between aboveground and belowground composition has usually been evaluated only at the community level (Hopfensperger 2007) however, similarity between both components at smaller spatial scales has been little explored. Here we wish to improve our understanding on this patch effect on seed bank properties and, more specifically, how these seed reservoirs (patch effect on soil seed banks) are affected by the main biotic (i.e. herbivory) and abiotic (i.e. climate) filters and how they interact with the standing vegetation. With this in mind, we have conducted a field survey in the Ecuadorian Dry Mountain Scrub Ecosystem. This ecosystem is especially

suitable because the community is dominated by a unique nurse/engineer plant along a very long altitudinal gradient and it presents locations with different grazing pressure.

Our working hypotheses are based on the following points: i) Climate amelioration with altitude may increase seed bank density and richness by means of the improvement of above-ground vegetation performance and fertility; ii) this climate effect will most likely be modulated by herbivory; iii) we expect that under high abiotic and biotic stress conditions differences between transient and permanent bank will be small or null while the improvement of these conditions will mean an increase in the difference between these two banks; iv) we expect that under high stress the distance in richness between above-ground and below-ground would be larger and it would be modulated by grazing as well.

Methods

Study Site

The field work was undertaken in the Ecuadorian Dry Mountain Scrub Ecosystem, a scrubby variant of Tumbesian dry forests that spread from north Peru (Harlling 1979) to south Ecuador in inter-Andine valleys along a 1000 m altitudinal gradient (Espinosa et al. 2011). Mean annual temperature is 27.5°C (Catamayo airport; 1500 m), the average maximum temperature is 30.8°C (October) and the minimum average temperature is 17.9°C (June). Average precipitation and evapotranspiration are 383 mm/year and 1112 mm/year, respectively (Richter and Moreira-Muñoz 2005). Between May and December rainfall does not compensate for the local evapotranspiration which causes an intense water deficit. The geological substrate is conformed of paleozoic metamorphic rocks intermingled with volcanic and sedimentary rocks from the Cretaceous and Tertiary periods, that create basic (pH: 7.6), nutrient rich, sandy to stony soils.

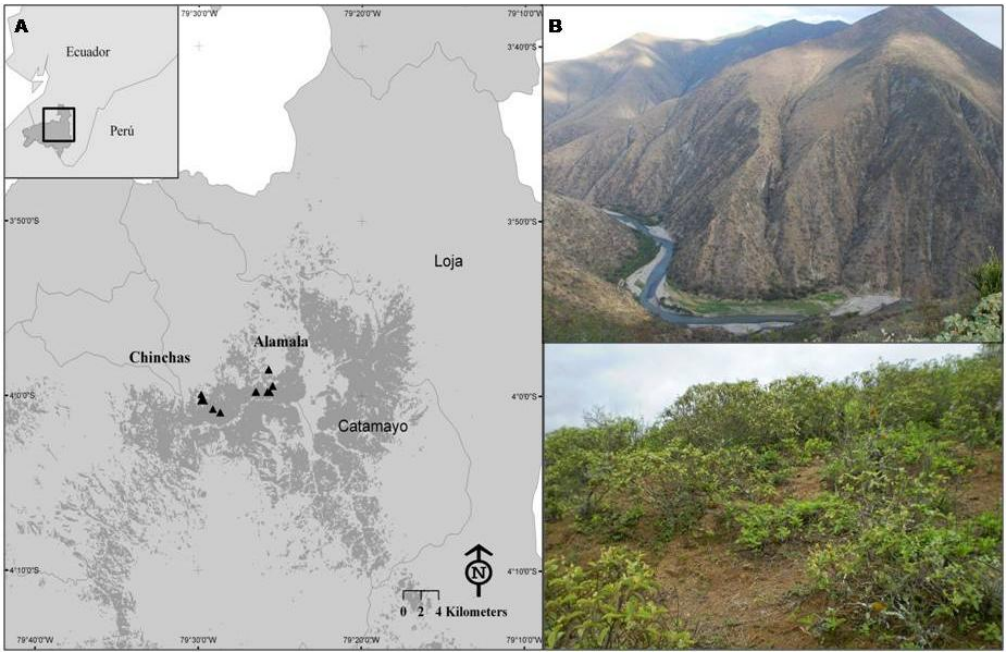

Figure 1.- A/ The dry mountain scrub ecosystem is represented in dark grey and the eight experimental sites are represented with black triangles. Half of them were located in Alamala (4º0'16.37"S; 79º29' 51.07"W) and the other half in Chinchas (3º59' 51.07"S; 79º26' 30.93"W) the coordinates correspond to the center of each location. B/ The dry shrub ecosystem and *Croton wagnerii* plants.

Vegetation forms conspicuous perennial patches interspersed in bare soil areas where annual plants are dominant in winter. *Croton wagnerii* (Müll) Arg. (Euphorbiaceae) is the dominant patch-forming scrub. *Croton wagnerii* is an evergreen shrub up to 2 meters high with autochorous or myrmecochorous seed dispersal (Jara et al. 2011). Other rare xerophytic and spiny species conform the vegetation patches together with *Croton* plants, such as some columnar cacti, *Euphorbia* species and some trees up to 7 m high such as *Acacia macracantha* Humb. & Bonpl. *ex* Willd. (Fabaceae), and *Bursera graveolens* (Kunth) Triana & Planch (Burseraceae) (Sierra 1999) (Figure 1).

Experimental design

We selected two localities 20 kms apart from each other in the valley of Catamayo (Loja; Ecuador); Chinchas with an altitude range from 1490 m to 2090 ml, and Alamala from 1530 m to 1950 m. They constitute an ideal natural system model to test our hypotheses because they share the same climate, slope, orientation, altitude range,

substrate and similar vegetation type differing only in their livestock density. Chinchas had a high livestock rate (1-3 heads/ha) whereas Alamala remained almost undisturbed. Cattle grazing occurs in winter at the maximum phenological peak of the vegetation. At each location we established four sites evenly distributed along the altitudinal gradient and at each site two 30 x 30 m plots were located less than 500 meters apart from each other (i.e, 16 plots, 8 per location). Climate conditions were more stressful at the lower edge with lower rainfall and higher temperatures. At the upper edge the dry scrub community is sharply transformed to a relatively moist forest (Richter and Moreira-Muñoz 2005).

Soil seed bank sampling

Three 10 x 10 cm soil samples and 3 cm in depth were collected in the upper, middle and bottom sides of each patch following the maximum slope, and the germination data obtained in the three of them was summed up to build our sampling unit. The upper 3 cm of soil were sampled since they accumulate most of the germinable seed bank in arid environments (Caballero et al. 2008).

We sampled the soil seed bank in 144 *Croton* patches in June 2010 (permanent seed bank) following seedling emergence and before seeds had been shed; the same patches were re-sampled in February 2011 after seeds had been dispersed and prior to seedling emergence (transient seed bank)- Total number of soil samples was 288. Soil samples were shredded and placed in 12 x 12 cm plastic cells in a greenhouse at average temperature of 25 ºC, the samples were irrigated each two days. The plastic cell contained a sterile substrate of pumice stone to maintain humidity of soil samples and a mesh to prevent the contact of soil with the pumice stone. Monitoring was conducted during 4 months; emerged seedlings were identified and removed, species that could not be identified were transplanted until identification was possible.

Vegetation Sampling

Vegetation was sampled at three different spatial scales. 1) At the whole plot scale (30 x 30 m). Vegetation richness was estimated by means of four 30-m long transects, parallel

to the slope and 8 m apart from each other in which we placed 20 contiguous 1.5 x 1.5 m quadrats. We recorded the presence and abundance of every perennial plant species in each quadrat and weighted averaged at the plot level. 2) At the patch scale. Presence and abundance of every perennial species was recorded together with the maximum patch length and width. 3) At neighbourhood scale. Distance between the target patch and the five nearest patches was measured and species occurrence inside the patches was also recorded. We calculated the maximum, average and minimum distances to neighbouring patches.

Biotic indices

We implemented some biotic indices based on the Relative Interaction Index (RII, (Armas et al. 2004) normally used to measure biotic interactions. In this study, we built five indices in order to measure the dominance between transient and permanent seed banks along gradients, and to estimate the importance between below-ground (i.e soil seed bank) and above-ground (i.e standing vegetation) species richness at three spatial scales.

Changes in the relationship between transient and permanent seed banks were measured using the Relative Dominance index (RDI) ($\mathrm{RDI} = \frac{\mathrm{TSB}-\mathrm{PSB}}{\mathrm{TSB}+\mathrm{PSB}}$). One index for seed abundance (RDIa) and another one for species richness (RDIr) were calculated being, TSB for the value corresponding to the Transient Seed Bank and PSB for the Permanent Seed Bank. This index ranges from –1 to 1, with positive values indicating transient seed bank dominance and negative values permanent seed bank dominance. To estimate changes in the relationship between seed bank and above-ground species richness we also built three indices (for each spatial scale) based on the following formula: RDI ($\mathrm{RDI} = \frac{\mathrm{SB}-\mathrm{AGV}}{\mathrm{SB}+\mathrm{AGV}}$) being SB the total seed richness considering June and February seed banks together and AGV is aboveground vegetation species richness. Indices were built at plot (RDIpl), neighbor (RDIn) and patch (RDIpt) scales. These indices range also from –1 to 1, with positive values indicating seed bank richness dominance and negative values standing vegetation richness dominance. In order to evaluate differences in species composition between aboveground vegetation and belowground seed banks

(transient plus permanent) at plot scale, the Sørensen dissimilarity index $\left(\frac{b+c}{2a+b+c}\right)$ was calculated, where *a* is number of shared species in two sites and the numbers of species unique to each site are *b* and *c*. The Sørensen index was chosen because it is simple, effective, and widely used (Magurran 2004). It was calculated using the "vegan" function in R (Oksanen et al. 2010).

Data Analysis

Nonlinear least-squares mixed models were used to model seed abundance and species richness both in the transient and permanent seed banks, as well as the biotic indices (RDI). Altitude, grazing and their interaction were considered as fixed factors. The convenience of including the quadratic terms of altitude and of the altitude-grazing interaction to account for non-monotonic responses along the gradient was evaluated. We included average distance to neighboring patches (averD), patch area (Area_pch), and plant species richness at the plot, neighborhood and patch levels as fixed factors. Plot was considered a random factor in order to account for spatial autocorrelation and other potential biases due to some unobserved trends related to our field experimental design (Warren 2010). We modeled the Sorensen index at plot level with nonlinear least-squares models with altitude, grazing and their interaction as fixed factors.

As most of the responses that we recorded were asymptotically bounded between a minimum and a maximum value, we used non-linear regression (Ritz and Streibig 2008) to fit models based in 2-parameter logistic functions (i.e., $= \frac{e^{a+bx}}{1+e^{a+bx}}$), expanded an translated to fit the responses between the corresponding bounding limits (Legendre and Legendre 1998). Assuming a logistic response is mostly analogous to the usual approach in ecology of fitting binomial GLM's to proportions or to responses bounded between 0 and 1 (Crawley 2007) but additionaly this releases the analysis from the need to transform the data in order to fit any of the probability distributions usually assumed by GLM's (Warton and Hui, 2011, Ohara y Kotze, 2010). We performed the usual model diagnostics and when apparent violations were found, we refitted the standard errors of the coefficients by adjusting the estimated variance-covariance matrix by means of sandwich estimators (White 1996).

Statistical analysis was performed with the R packages stats, nlme (Pinheiro and Bates 2000) and nls (Bates and Chambers 2002).

Results

In this study, 2842 seedlings of 15 species emerged from the transient seed bank and 1286 seedlings of 16 species from the permanent seed bank. Average species richness per sample was very similar in transient (2.9 species) and permanent (2.8 species) seed banks, ranging from 0 to 7 or 8 species respectively. Seed density was lower in the permanent seed bank (330 seeds/m^2 in average, ranging from 0 to 2296 seeds/m^2) than in the transient one (mean of 731 seeds/m^2, ranging from 0 to 5185 seeds/m^2). We detected 22 species, 10 of which (3 perennials and 7 annuals) appeared in both seed banks, 6 species (5 perennials and 1 annual) were only present in the transient seed bank and 6 species (all of them perennials) only occurred in the permanent seed bank.

Effects of altitude and grazing on transient and permanent seed banks

Altitude, grazing and their interaction exerted a significant effect on species richness and seed abundance of the transient seed bank; however, no significant effect was observed on the permanent seed bank (Table 1). Grazing promoted seed species enrichment and higher seed densities at the more stressful lowland areas. Along the altitudinal gradient both seed bank attributes slightly decreased in the grazed locations; nevertheless, in the undisturbed locations, species richness and seed abundance increased four- and six fold, respectively, towards higher and milder elevations (Figure 2). Annual plants showed the same response to both abiotic and biotic stressors except for the lack of response of the proportion of annual seed abundance to altitude (Table 1).

Effect of aboveground vegetation at different spatial scales on the permanent and transient seed banks

None of the standing plant richness variables measured at different scales affected seed species richness in both seed bank compartments. Aboveground richness only exerted a

meaningful effect at the patch scale, being seed abundance larger in species-rich patches. The further the distance to neighboring patches the greater the seed abundance in the target patch (table 1). Surprisingly, patch area had a negative effect on seed abundance of the permanent seed bank. In contrast, the proportion of annual species in the seed bank showed no effect of plant richness at patch scale but it showed high effect of plant richness at plot scale, and contrary to the response of the seed bank the proportion of annual seeds diminished if the distance to neighbors increased (Table 1).

Fixed Effects	**Transient Seed Bank**				**Permanent Seed Bank**			
Seed bank	**Richness**		**Abundance**		**Richness**		**Abundance**	
(Intercept)	37.81463	**	-11.59682		-3.98738	**	-3.41087	
Altitude	-0.04830	***	0.00487	***	0.00116		-0.00003	
Altitude2	0.00001	***	n.i		n.i		n.i	
Grazing	-32.23807	**	10.27228	***	2.49579		0.64309	
Altitude:Grazing	0.04149	**	-0.00524	***	-0.00116		-0.00001	
Altitude:Grazing2	-0.00001	**	n.i		n.i		n.i	
AverD	0.06192		0.27619	***	0.02817		0.36934	***
Rich_Patch	0.04629		0.14498	**	0.09254		0.39521	***
Rich_neib	-0.08897		-0.00371		0.01270		0.06529	
Rich_plot	0.01255		0.02185		0.04811		0.04955	
Area_patch	-0.03261		-0.08379		-0.05170		-0.24285	***
b) Annual species seed bank	**Richness**		**Abundance**		**Richness**		**Abundance**	
(Intercept)	41.68171	**	-3.60363		40.13572		125.32309	**
Altitude	-0.05300	**	0.00157		-0.04310		-0.13985	**
Altitude2	0.00002	**	n.i		0.00001		0.00004	**
Grazing	-63.12424	***	9.96581	***	-60.84226	**	-114.39012	
Altitude:Grazing	0.07620	***	-0.00522	***	0.06842	**	0.13082	
Altitude:Grazing2	-0.00002	***	n.i		-0.00002	**	-0.00004	
AverD	0.17045		-0.00821		-0.03598		-0.23060	
Rich_Patch	0.06884		0.27579		-0.13150		-0.45506	
Rich_neig	-0.06896		-0.82378	***	-0.06471		-0.02775	
Rich_plot	0.04740	***	0.27606	***	-0.03793		-0.03285	
Area_ptch	-0.00765		-0.06360		0.04919		0.16723	

Table 1: ***Estimates of nonlinear mixed-effects models for the whole seed bank richness and abundance***. (a) and for the proportions of annual species richness and abundances (b) in the transient and permanent seed banks. Plot identity was used as a random factor. Altitude2: the cuadratic term of altitude. Altitude:Grazing: interaction between altitude and grazing. AverD: average distance between the target patch and the five nearest patches, Rich_Patch: plant richness in the target patch, Rich_neib: plant

richness in the five nearest neighbor patches. Rich_plot: plant richness in the plot and Area_patch: patch area. The significance is shown as *** <0.01, ** <0.05. n.i; Variables not included in the model.

Dominance shifts between the transient and permanent seed banks along co-occurring stress gradients

The relationship between species richness in the transient *vs.* the permanent seed banks was not affected by altitude (RDIr, Table 2); however, in terms of abundance, the dominance of the transient seed bank increased towards higher altitudes. Under grazing conditions, although the permanent seed bank showed more species than the transient one (especially at high altitudes), seed abundance was greater in the transient seed bank. The interaction between altitude and grazing showed an interesting response of the Relative Dominance Indices in terms of richness and abundances (RDIr, RDIa). Under ungrazed conditions at higher elevations (higher productivity conditions), the transient seed bank was more species-rich than the permanent one. On the contrary, under grazing conditions, at the edges of the altitudinal gradient seed richness was almost similar in both seed banks (transient *vs* permanent) while at middle altitudes the transient seed bank was richer in species than the permanent one (Figure 3). In terms of seed abundance, the dominance of the transient seed bank increased along altitude in ungrazed conditions (RDIa); however, the opposite occurred under grazing conditions being the RDIa index reduced along altitudinal gradient until seed abundance was nearly the same in both seed banks.

	RII Total Seed Bank			
Fixed Efects	**Richness**		**Abundance**	
(Intercept)	32.35292		-5.52887	**
Altitude	-0.03836		0.00350	***
Altitude2	0.00001			
Grazing	-59.49560	**	8.06796	***
Altitude:Grazing	0.07019	***	-0.00442	***
Altitude:Grazing2	-0.00002	***		
AverD	0.03458		0.03720	
Rich_Patch	0.06537		0.08228	
Rich_neib	-0.05091		0.09487	
Rich_plot	-0.00422		-0.01456	
Area_ptch	-0.06031		-0.04251	

Table 2: ***Estimates of nonlinear mixed-effects models for RDI indices.*** The RDI was calculate between the transient vs. the permanent seed banks of richness and abundance (see methods for more details on these indices). AverD: average distance between the target patch and the five nearest patches, Rich_Patch: plant richness inside the target patch, Rich_neib: plant richness in the five nearest neighbor patches. Rich_plot: plant richness in the plot and Area_ptch: area of the target patch. The significance is shown as *** <0.01, ** <0.05. n.i; Variables not included in the model.

Dominance shifts of aboveground vs. *belowground richness and species composition along co-occurring stress gradients*

In general terms, vegetation richness was higher than seed bank richness. Dominance between aboveground vegetation richness *vs.* belowground seed richness greatly varied along the altitudinal gradient and at different grazing intensities, but in a different way depending on the spatial scale (Table 3). At patch level, in the ungrazed location belowground species richness dominated at low altitudes and this relationship shifted to be dominated by vegetation species richness along the altitudinal gradient, however, aboveground and belowground species richness was highly similar under grazing conditions all along the altitudinal gradient (Figure 4). A similar trend was also observed at the neighborhood scale for ungrazed locations, but under grazing conditions at both edges of the altitude range the seed bank and neighbor species richness were very similar. At plot level, only a slight effect of altitude was observed on the Relative dominance index (Figure 4). Finally, the Sorensen dissimilarity index between aboveground and belowground species composition in terms of presence absence data was 0.61 both in grazed and ungrazed conditions. This index was not affect by any of the studied variables (Table 3).

	RII Index					Sorensen index
Fixed Efects	**RDIpatch**		**RDIneighbor**		**RDIplot**	
(Intercept)	-4.72658	***	-20.24755		-5.29339	***	1.96100
Altitude	0.00251	**	0.02054		0.00181	**	-0.00090
Altitude2	n.i		-0.00001		n.i		n.i
Grazing	4.93797	**	61.22298	**	2.23028		0.15810
Altitude:Grazing	-0.00274	**	-0.06809	**	-0.00128		-0.00003
Altitude:Grazing2	n.i		0.00002	**	n.i		n.i
AverD	0.12643		0.04813		0.08666		n.i
Area_ptch	-0.05800		0.00406		-0.05679		n.i

Table 3. ***Coefficient estimates by means of nonlinear mixed-effects models on RDI***. The Relative Dominance Indices at three spatial scales; patch (RDIpatch), five nearest patches (RDIneighbor) and plot (RDIplot). AverD: average distance between the sampled patch and the five nearest patches, Area_ptch: sampled patch area. The significance is shown as *** <0.01, ** <0.05. n.i; Variables not included in the model were not significant.

Discussion

As expected our study demonstrates that climate acted as a key environmental filter in soil seed bank development and structure and also that grazing modulated the effect of climate on seed bank properties. In this tropical dry scrub, richness and abundance of seeds increased along the altitudinal gradient, most likely because environmental conditions improved with altitude (Richter and Moreira-Muñoz 2005) , and it determined greater plant primary productivity and, eventually, greater seed production and an increase in the transient seed bank. Other studies carried out in Alpine mountains and Arctic ecosystems reported a decrease in seed bank richness and abundance with altitude (Funes et al. 2003; Ma et al. 2010); however these ecosystems, contrary to mountain tropical dry ecosystems, are characterized by increasing climatic stress with altitude (a shorter period of vegetative growth in alpine and arctic mountains with altitude) that greatly constraint seed production (Thompson 1985).

Few studies (Ortega et al. 1997, Ma et al. 2010a) have evaluated the simultaneous effect of grazing and climatic conditions on the seed bank performance. Our study demonstrated that the effect of grazing highly depends on climatic conditions. At the more stressful lower altitudes, grazing increased richness and abundance of seeds in the transient seed bank. The mechanisms underlying these results may lie on two non-exclusive effects of cattle on vegetation, on one hand (Russi et al. 1992)) found that grazing promoted flower and fruit production and on the other hand Vignolio & Fernandez (2010) observed that cattle acted as a vector of dispersal for many plant species.

Although seed abundance and richness in the transient seed banks gradually increased along altitude, this trend was profoundly modified by grazing, i.e. it reduced seed bank richness at high elevations comparing with the ungrazed conditions. Previous studies in the study area have shown a decline in aboveground richness and plant cover with altitude (Espinosa et al in prep.), since changes in seed bank richness are usually linked to above-ground vegetation shifts (Ortega et al. 1997), this would explain the steep drop in seed species richness detected at high altitudes.

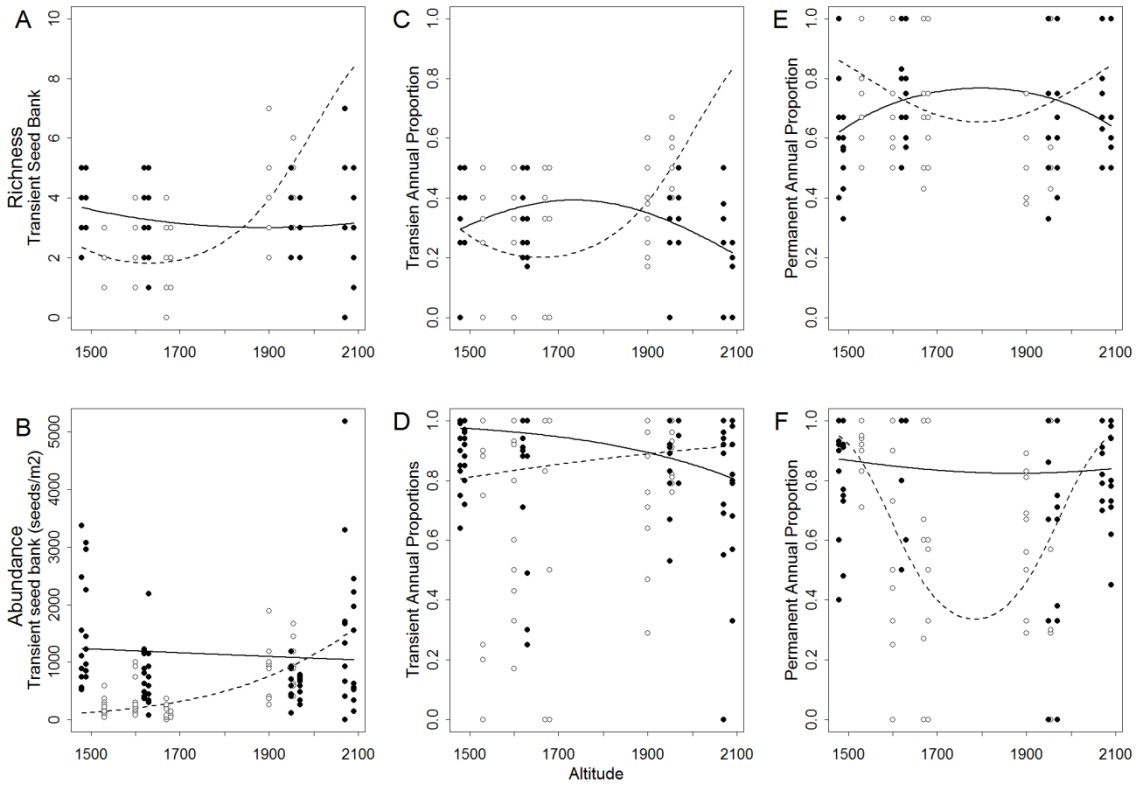

Figure 2: Fitted curves of nonlinear mixed-effects models (nlme) in the transient and permanent seed banks. Total seed richness (A) and abundance (B) in the transient seed bank. Proportion of annual species abundance (C) and richness (D) in the transient seed bank. Proportion of annual species abundance (E) and richness (F) in the permanent seed bank. Patches are represented with circles, black circles represent the grazing patches and white circles the undisturbed ones. Fitted curves are shown for each location, solid line for the grazed location and dotted line for the undisturbed one.

Nevertheless, we did not detect any effect of altitude on the permanent seed bank. Most likely, the effect of altitude might have been overridden due to a decrease in seed longevity in the more benign environmental conditions (Cavieres and Arroyo 2001). Seed longevity is usually affected by soil moisture content, since it enhances fungal infection and predation of seeds (Funes et al. 2003). The decline in species richness and abundance in lower and drier areas could be related to shifts in the aboveground vegetation structure with a decrease in the presence of annual plants together with the dominance of perennial plants which usually reproduce in a vegetative way rather than sexually in areas of great environmental stress (Milton 1939, Thompson 1985, Ma et al. 2010b).

Grazing caused a decrease in total species richness and in the annual species proportion together with an increase in seed abundance. This result was probably directly related to changes induced at the plant community level by grazing pressure (Bertiller 1998, Kinloch and Friedel 2005), but also to changes in the performance, abundance and the reproductive success of each species (Pazos et al. 2007, Kinucan and Smeins 2008). Most likely, the reduction in interspecific competition through grazing pressure on palatable perennials (Bestelmeyer et al. 2003) together with the gap creation that favored annual plant establishment (Navie et al. 1996), promoted the high seed abundance and the low species richness in the seed bank.

The average distance to neighboring patches had an unexpected positive effect in the abundance of both seed banks. This could be due to two non-exclusive mechanisms, on one hand most species of this dry ecosystem have wind-dispersed seeds (Jara-Guerrero et al. 2011), and on the other hand secondary dispersal on the soil surface due to run-off may have swept away superficial seeds being the more isolated shrubs the ones that collected more seeds.

Patch size negatively affected the abundance in the permanent seed bank. This decline could be explained due to the effect of large seed clusters attracting seed predators such as rodents.

Relationship between the transient and the permanent soil seed banks

Changes in the intensity of co-ocurrence of both biotic and abiotic stressors seem to induce a shift in the dominance between the transient and the permanent seed banks. Under ungrazed conditions, richness and abundance of the transient seed bank became dominant at high altitudes (less stress) whereas at the more stressful conditions of lowland areas the transient and the permanent seed banks showed similar seed abundance and number of species. The development of the permanent and transient seed banks are largely influenced by seed production of the aboveground vegetation and seed longevity in the soil (Cavieres and Arroyo 2001, Ma et al. 2010a).Thus, the rainy climate of high altitudes may have promoted seed production (Ortega et al. 1997)

together with a decrease in seed longevity soil (Cavieres and Arroyo 2001), and consequently, it may have increased the contribution of the transient seed bank in relation to the permanent one. On the other hand, under stressful climate conditions the aboveground vegetation may produce fewer seeds but, dry conditions may enhance seed longevity, and consequently, both factors together will most probably have induced the permanent and the transient seed banks to be very similar in richness (Ortega et al. 1997). However, this effect was completely overridden by grazing, since in this study we observed that at the high stressful conditions of lowland areas, both seed banks showed similar richness values.

In addition the seed bank abundance under grazing pressure showed an increase in the dominance of the transient seed bank which suggest a stimulation of flower and fruit production by grazing (Russi et al. 1992) or a more efficient distribution of propagules due to cattle . This patent effect was modulated along climate gradients, thus at higher stress conditions grazing increased the transient seed bank dominance in comparison with the ungrazed conditions.

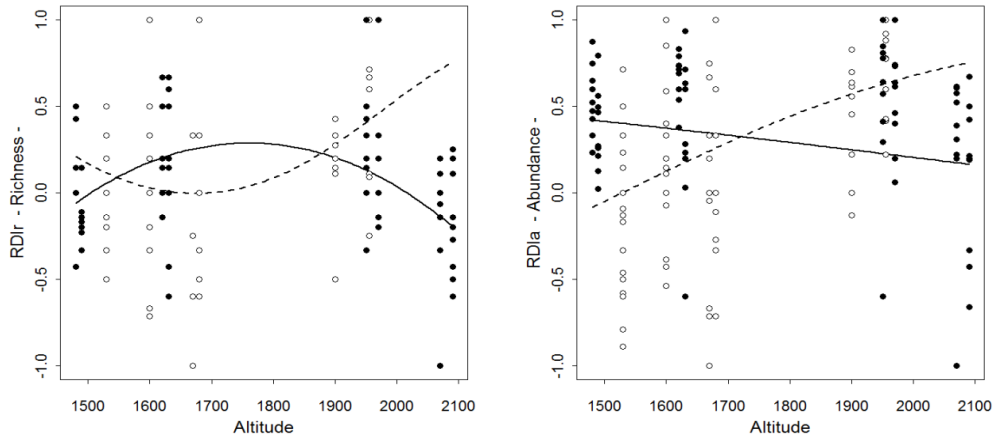

Figure 3: Fitted curves of nonlinear mixed-effects models (nlme) on the Relative Dominance Indices between the transient and the permanent seed banks in terms of richness (RDIa) and abundance (RDIr). Target patches are represented as circles, black circles are grazed patches and white circles are undisturbed ones. The fitted curves are shown for each location, solid line for grazed location and dotted line for undisturbed location.

Relationship between above-ground vs. below-ground species richness and composition

Dominance between aboveground vs. belowground species richness greatly varied along the altitudinal gradient and grazing intensities, but in a different way depending on the spatial scale. Grazing maintained the relationship of aboveground vs belowground richness at similar values all along the altitudinal gradient. At low altitudes (high stress) grazing reduced the dominance of standing vegetation, while at higher altitudes (less stress) grazing reduced seed bank dominance. According to Espinosa et al. (in prep.) vegetation showed high species richness at low altitudes that increased along the altitudinal gradient. Grazing changed this pattern, in benign conditions grazing drives a reduction in the competition and an increase of diversity in the above-ground standing vegetation (Espinosa et al. in prep.) which would increase of above-ground vegetation richness. In stressful conditions the grazing reduced the above-ground patch diversity (Espinosa et al. in prep.) and consequently, it reduced the patch dominance in stressful locality.

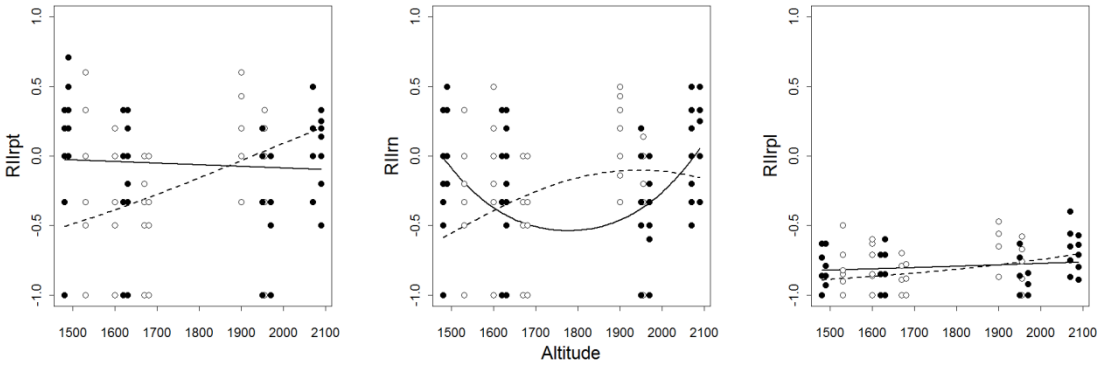

Figure 4: Fitted curves of nonlinear mixed-effects models (nlme) RDI indices at three spatial scales of the aboveground vegetation; A) patch (RDIpatch), B) neighbor patches (RDIneighbor) and C) plot (RDIplot). Target patches are represented as circles, black circles are grazed patches and the white circles are undisturbed patches. Fitted curves are shown for each the location, solid line for grazing location and dotted line for the undisturbed location.

In conclusion, our results show an important interaction between stressors, the effects in the soil seed bank is better explained when both climatic and grazing stressors are

evaluated. In undisturbed conditions the richness and abundance of seed bank increases with altitude and their consequent stress amelioration. This observed pattern is modulated by grazing, in the lower end of altitude gradient grazing produce an increase in the richness and density seed bank and in the higher end of altitudinal gradient the grazing reduces this two attributes. Finally our results also are in agreement with our working hypothesis, the differences between transient and permanent seed banks are affected by both stressors, the plant performance in benign climatic conditions allow higher seed input, increase the dominance in transient seed bank, while the higher stress conditions increase the longevity of seeds, reducing the transient seed bank dominance. Changes in this patters produces by grazing are linking with changes in the above-ground vegetation.

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Conclusiones generales

El trabajo de investigación desarrollado en la presente tesis ha permitido establecer las siguientes conclusiones generales:

Los bosques tropicales estacionalmente secos

- El ensamble de especies en los bosques tropicales secos está controlada principalmente por la altitud (proximidad al ecotono bosques de montaña) y la disponibilidad de agua, estas variables determinan la estructura florística de la comunidad.

- La disponibilidad de agua mostró ser un factor determinante de la riqueza, encontrándose que las áreas que poseen mayor riqueza son aquellas que poseen una menor disponibilidad de agua. Esta respuesta es coherente con la Hipótesis de la Gradiente de Estrés ya que el incremento de las relaciones de facilitación estaría incrementando la cantidad de especies que coexisten a nivel local.

- Contrariamente a la hipótesis de neutralidad propuesto por Hubbell nuestros resultados muestran que en el ecosistema de bosque seco tropical las relaciones positivas planta-planta son una forma importante de mantener la diversidad. A diferencia de otros trabajos desarrollados en otros ecosistemas tropicales la respuesta observada en el bosque seco muestra que en ecosistemas con alto estrés las interacciones positivas tienden a predominar.

- Las especies de bosque seco tropical muestran un bajo grado de agrupamiento con sus congéneres, lo cual coincide con la propuesta de la "*Dependencia Negativa de la Densidad*" propuesta por Janzen – Connell. Esta respuesta contribuye a la predominancia del comportamiento acumulador de las especies en este ecosistema. Curiosamente, el comportamiento de las especies cambia en función de su tamaño, se observa que los individuos grandes y pequeños funcionan independientemente el uno del otro.

Matorral seco tropical

- Los resultados muestran que la magnitud de los efectos de las especies ingenieras del ecosistema en la diversidad y la productividad de la comunidad vegetal varían a lo largo de gradientes de estrés climático y con la escala espacial de la comunidad. Así, en las zonas con mayor presión ambiental y una mayor presión de pastoreo, el efecto de las plantas ingenieras es mayor.

- La estabilidad de la diversidad en la escala de la comunidad parece ser la norma con efectos nulos de los factores de estrés en las propiedades de la comunidad. Esto es sorprendente, ya que hemos detectado la existencia de efectos netos a escalas más pequeñas de la comunidad. Tomados todos estos resultados juntos podemos suponer que la dinámica de compensación es la responsable de la estabilidad de la comunidad a lo largo de gradientes ambientales nítidas, incluso cuando dos factores de estrés co-ocurren.

- A nivel de microhábitat la importancia de la facilitación incrementa cuando los factores de estrés climático aumentan. Bajo las copas de Croton, la diversidad y la cobertura es mayor que en el suelo desnudo, esta diferencia se incrementa con el estrés abiótico. Esta respuesta fue modulada por el pastoreo, así en las zonas más altas con menor estrés climático, la facilitación se mantuvo debido a una reducción de la competencia por efecto del pastoreo. Así, el estrés biótico producido por los herbívoros altera significativamente la naturaleza y la fuerza de las interacciones, pudiendo incluso cambiar el signo de las interacciones de las comunidades vegetales.

- Los resultados obtenidos con el banco de semillas muestran una importante interacción entre los factores de estrés, los efectos en el banco de semillas del suelo se explica mejor cuando los factores de estrés, tanto climáticos y el pastoreo son evaluados. En condiciones inalteradas la riqueza y abundancia del banco de semillas aumenta con la altitud y la reducción del estrés. Este patrón es modulado por el pastoreo, en el extremo inferior del gradiente altitudinal, el pastoreo produce un aumento en la riqueza y la densidad del banco de semillas,

en el extremo superior de un gradiente altitudinal del pastoreo reduce estos dos atributos.

- Las diferencias entre los bancos de semillas transitorios y permanentes se ven afectados por factores de estrés, el rendimiento de la planta en las zonas con condiciones climáticas benignas permiten una mayor entrada de las semillas, aumentando el dominio del banco de semillas transitorio, mientras que en condiciones más estresantes la longevidad de las semillas aumenta, reduciendo el predominio del banco de semillas transitorio. Los cambios producidos por el pastoreo en estos patrones están vinculados con los cambios en la vegetación sobre el suelo.